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PHYLOGENETIC RELATIONSHIPS OF *LIPINIA* (SCINCIDAE) FROM NEW GUINEA BASED ON DNA SEQUENCE VARIATION FROM THE MITOCHONDRIAL 12S rRNA AND NUCLEAR *C-MOS* GENES

Christopher C. Austin

Evolutionary Biology Unit, South Australian Museum, Adelaide, South Australia 5000 Australia.

Present Address: The Institute of Statistical Mathematics,
4-6-7 Minami-Azabu Minato-ku, Tokyo 106-8569, Japan.

Email: caustin@ism.ac.jp

(with two text-figures)

ABSTRACT.- A molecular phylogenetic analysis of four species of *Lipinia* from New Guinea, and one species from the Palau archipelago, is presented based on DNA sequence variation from seven hundred and eleven aligned sites from the mitochondrial 12S rRNA and nuclear *c-mos* genes. There is strong support for the basal placement of *Lipinia leptosoma* from Palau, resulting in a monophyletic New Guinean clade. Previous hypotheses of relationships suggested a New Guinean origin of the genus *Lipinia*. These results, however, suggest that *Lipinia* may have biogeographic origins in the Philippines or south-east Asia rather than New Guinea.

KEY WORDS.- Biogeography, data-partitions, likelihood, Lygosominae, multiple datasets, Pacific, Papua, Scincidae.

INTRODUCTION

The genus *Lipinia* includes 21 species with two centres of species abundance. Eight described species occur in the Philippines (Greer, 1974; Brown and Alcalá, 1980) and seven described species occur in New Guinea (Greer, 1974; Zweifel, 1979; Greer and Mys, 1987; Austin, 1995). One species, *Lipinia noctua*, has a large range that extends from the Papuan region throughout Oceania to the Hawaiian Islands in the north-east and Easter Island and Pitcairn Island in the south-east. The remaining species occur in the Indonesian region with only one species reaching mainland south-east Asia (*L. vittiger*). The phylogenetic affinities of *Lipinia* with other lygosomine scincid genera is unclear, but Greer (1974) suggests a close relationship between *Lipinia* and three other genera from New Guinea (*Lobulia*, *Papuascincus*, and *Prasinohaema*). This phylogenetic relationship would suggest a Papuan origin for *Lipinia* with a subsequent invasion into island south-east Asia and radiation in the Philippines. A recent description of the monotypic genus *Paralipinia*

from Vietnam, however, provides some evidence that *Paralipinia* is the sister taxa to *Lipinia* and suggests that *Lipinia* has origins in south-east Asia, and quite possibly mainland Vietnam (Darevsky and Orlov, 1997). In addition to *Lipinia*, *Lobulia*, *Papuascincus*, and *Prasinohaema* Greer's 'group I' includes *Scincella* and *Ablepharus*. The last two genera have broad distributions including south-east Asia, and *Lipinia* may have closer affinities to these taxa than to the New Guinea genera.

In this paper I examine the phylogenetic relationships of certain *Lipinia* species from the Papuan region to address questions concerning intrageneric relationships and biogeography. A hypothesis of phylogenetic relationships is based on DNA sequence variation from two genes: the mitochondrial ribosomal RNA 12S gene and the single-copy nuclear proto-oncogene *c-mos*. Mitochondrial genes, and the 12S rRNA gene in particular, have been widely used because of their ability to recover phylogenetic relationships. Nuclear genes suitable for phylogenetic use, however, have been

far more difficult to identify. Graybeal (1994), however, distinguished several potential nuclear candidate genes that might prove useful for vertebrate phylogenetic reconstruction. The single copy nuclear proto-oncogene *c-mos*, one of the genes identified by Graybeal (1994), has recently been shown to be a useful phylogenetic marker for resolving squamate relationships (Saint et al., in press).

MATERIALS AND METHODS

Specimens and tissue samples.—Muscle and liver tissue samples were dissected from freshly sacrificed specimens and either stored at -80 °C or in 70% ethanol. Specimens and tissue samples were collected for the following five species (Figure 1): *Sphenomorphus leptofasciatus* (Texas Natural History Collection [TNHC 51918]), from Madang Province, Papua New Guinea. *Lipinia rouxi* (TNHC 51436), from the Lelet Plateau, New Ireland Island/Province, Papua New Guinea. *Lipinia longiceps* (TNHC 51284), from Garaina Valley, Morobe Province, Papua New Guinea. *Lipinia pulchra* (TNHC 51290), from Garaina Valley, Morobe Province, Papua New Guinea. *Lipinia leptosoma* (presently being catalogued at the California Academy of Sciences; field number RNF 415), from Babeldaob Island Palau.

Although there is support for the close relationship among *Lipinia*, *Lobulia*, *Prasinohaema* and *Papuascincus*, there is some doubt as to the monophyly of these genera. *Sphenomorphus leptofasciatus*, therefore, was chosen as a conservative outgroup (Greer, 1974).

DNA isolation, amplification, and sequencing.—Isolation of DNA from either muscle or liver tissue was conducted following the protocols of Hillis et al. (1990) with one exception. Tissue samples were not ground in a mortar and pestle with liquid nitrogen. Rather, ~50 mg of tissue was digested with 20 (1 of 10 mg/ml proteinase K for three hours.

Double-stranded DNA products were amplified following the protocols of Palumbi et al. (1991). For the 12S gene two oligonucleotide primers synthesized at the South Australian Museum were used with the polymerase chain reac-

tion (PCR) to amplify and sequence both complementary strands. The 12S primers used were: forward SAM(M1): 5'-TGA CTG CAG AGG GTG ACG GGC GGT GTG T-3' and reverse SAM(M2): 5'-AAA AAG CTT CAA ACT GGG ATT AGA TAC CCC ACT AT-3'. The nuclear *c-mos* primers (Saint et al., in press) used were: forward SAM(G73) 5'-GCG GTA AAG CAG GTG AAG AAA-3' and reverse SAM(G74) 5'-TGA GCA TCC AAA GTC TCC AAT C-3'.

Double-stranded PCR products were amplified using a Corbett FTS 320 Thermal cycler. The specific thermal cycle used is as follows: (i) one cycle at 94 °C X 3 min, 47 °C X 1 min, and 72 °C X 1 min; (ii) thirty four cycles at 94 °C X 45 seconds, 47 °C X 45 seconds, and 72 °C X 1 min; (iii) one cycle at 72 °C X 6 min. PCR products were cleaned using BresaClean (Bresatec Ltd.) and then cycle sequenced on Corbett FTS1 Thermal cycler using ABI Prism dye-terminators (ABI) and protocols specified by the manufacturer. Sequences were determined on an ABI 377 DNA automated sequencer.

Phylogenetic analysis.—*Lipinia* belongs to the *Sphenomorphus* group of lygosomine skinks and trees were rooted using *Sphenomorphus leptofasciatus* as an outgroup (Greer, 1974).

Sequences from the 12S rRNA and *c-mos* genes were aligned using Clustal V (Higgins et al., 1991). Both parsimony and likelihood phylogenetic reconstruction methods were used as they are two of the most robust and accurate methods available (Felsenstein, 1981; Huelsenbeck and Hillis, 1993). The presence of a transition/transversion bias has been well documented with transitions occurring at a higher frequency than transversions (Brown et al., 1982; Vigilant et al., 1989; Knight and Mindell, 1993). Maximum likelihood was used to estimate the transition/transversion (TI/TV) ratio because estimation of the transition/transversion bias from the data themselves may underestimate the ratio due to multiple substitutions (Wakeley, 1996; Purvis and Bromham, 1997).

All phylogenetic analyses were done using PAUP* test version 4.0d64, written by D.L. Swofford. The two parameter HKY'85 model was implemented, which uses nucleotide fre-

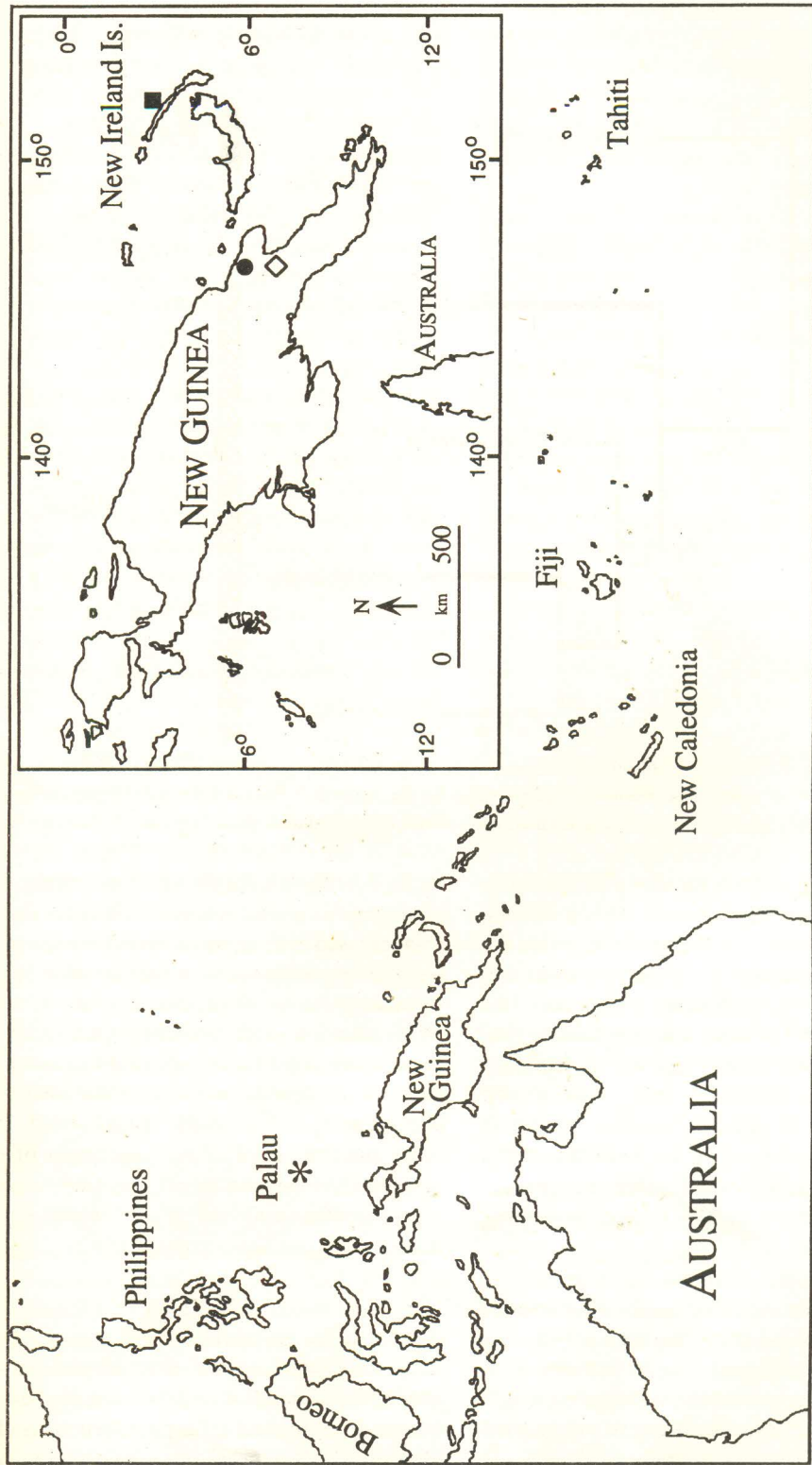


FIGURE 1: Map of sample localities used in this study: *Lipinia leptosoma*, denoted by asterisk; *Lipinia rouxi*, denoted by solid square; *Lipinia pulchra* and *Lipinia longiceps*, denoted by open diamond; *Lipinia nocuta* and *Sphenomorphus leptofasciatus*, denoted by closed circle.

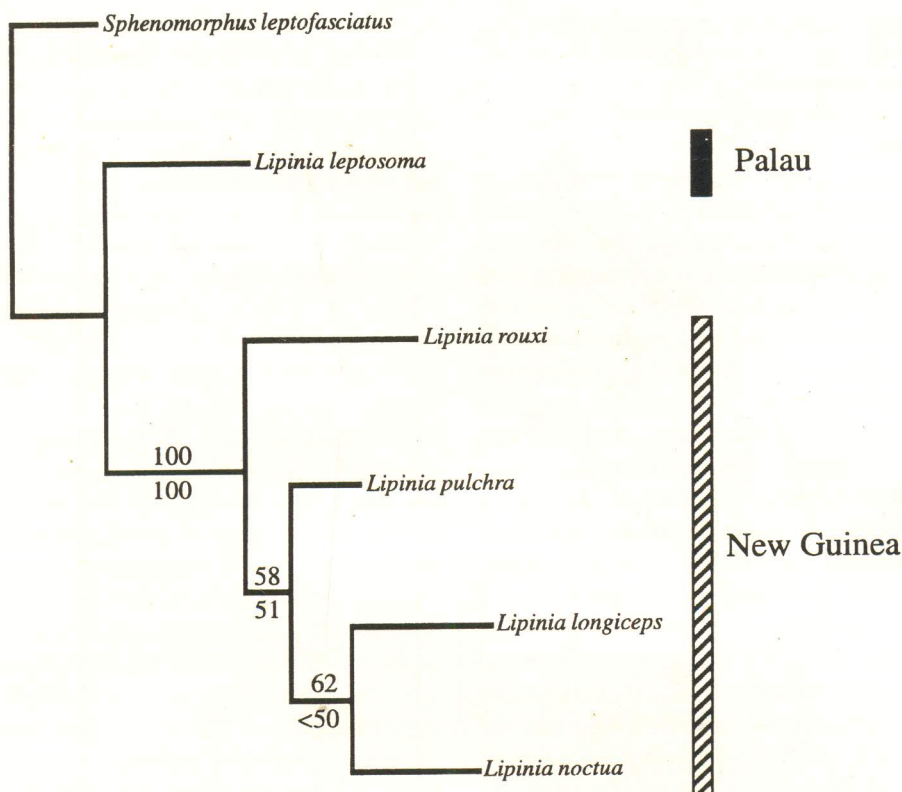


FIGURE 2: Phylogram, showing relative branch lengths, of the single maximum parsimony tree obtained from branch and bound PAUP* searches using *Sphenomorphus leptofasciatus* as the outgroup. Numbers at nodes represent bootstrap proportions for 1,000 and 100 pseudoreplicates for parsimony (above the line) and likelihood analyses (below the line).

quencies estimated from the data, for all likelihood analyses (Hasegawa et al., 1985). Branch and bound searches, which guarantee to find the shortest tree, were used for all parsimony analyses including the bootstrap replicates. The branch and bound method was also used to find the optimal likelihood tree. In order to facilitate a reasonable number of bootstrap pseudoreplicates for likelihood, which is computationally expensive, the heuristic search option was implemented. The tree bisection-reconstruction (TBR) branch swapping method was used.

The partition-homogeneity test was used to assess if both genes should be combined in a single analysis. The test examines heterogeneity by calculating the sum of the tree lengths from the original dataset and comparing that with the tree length distribution from pseudopartitions (of original partition size) [Huelsenbeck et al., 1996].

Phylogenetic Confidence.—Confidence in the phylogenetic signal for this molecular data set was assessed in three ways. First, both maximum parsimony and maximum likelihood were used to estimate a phylogenetic hypothesis (Kim, 1993). Second, both maximum parsimony and maximum likelihood analyses were bootstrapped to assess confidence for each node (Felsenstein, 1985; Swofford and Olsen, 1990; Hillis and Bull, 1993). Finally, presence of a significant phylogenetic signal was assessed using the *g*₁ statistic estimated from 100,000 random trees (Hillis and Huelsenbeck, 1992).

RESULTS

A total of seven hundred and eleven aligned sites, three hundred and fifty aligned sites for 12S and three hundred and sixty one aligned sites for *c-mos*, were used in the phylogenetic analysis (Appendix I). Of these, eighty two sites were in-

formative under the parsimony criterion. For the entire data matrix a TI/TV ratio of 1.96 was estimated using maximum likelihood. This TI/TV ratios was used as a weighting scheme in all phylogenetic analyses. The partition homogeneity test was non-significant ($P = 1.0$), indicating datasets from the two genes should be combined.

Insertion/deletion (indels) events are present in the alignment for both genes. *c-mos* is a protein-encoding gene and an open reading frame was observed for all taxa. As expected, indels present in *c-mos* are in multiples of three nucleotides (corresponding to a single codon), thus preserving the reading frame. For *c-mos* a two codon (six nucleotide) deletion was observed for *Lipinia pulchra*, and a single codon (three nucleotide) deletion was observed for *L. noctua* (Appendix I). As the ribosomal 12S gene is not a protein-encoding gene, indels need not be in multiples of three nucleotides.

The single maximum parsimony (MP) tree is presented with bootstrap support from both the MP and maximum likelihood (ML) analyses (Fig. 2). Bootstrap proportions in Fig. 2 are for 1000 and 100 pseudoreplicates, for MP and ML respectively. There is strong bootstrap support (100) for the basal placement of *Lipinia leptosoma* from Palau rendering the New Guinea species monophyletic. The matrix for both uncorrected and HKY'85 corrected genetic distances, is presented in Table 1. The g_i (estimated from 100,000 randomly generated trees) was -1.41, indicating significant phylogenetic signal ($P 0.01$) [Hillis and Huelsenbeck, 1992]. For the parsimony analysis, the tree length was 258.4 with a consistency index (CI) of 0.854. For the

likelihood analysis the likelihood value was -1963.6. Fractional tree length and likelihood values for the parsimony and likelihood analyses result from a fractional estimate of the transition/transversion ratio.

DISCUSSION

Zweifel (1979) synonymized *Lipinia rouxi* with *L. nocuta*, but non-traditional morphological data by Greer and Mys (1987) and allozyme data by Austin (1995) showed that *L. rouxi* is clearly a distinct species. The results of both Greer and Mys (1987) and Austin (1995), however, were equivocal as to whether *L. rouxi* was the sister to *L. noctua*. The results from this study further demonstrate the specific status of *L. rouxi* from New Ireland Island as well as provide support that *L. rouxi* is basal within the New Guinea clade.

Based on the molecular data presented in this paper, the New Guinean *Lipinia* are monophyletic. Three additional species of *Lipinia* are recorded from New Guinea, however, these species either have isolated ranges or are known from just a few specimens and were not included in the analysis. *Lipinia cheesmanae* is known from only four specimens, the holotype from the Cyclops Mountains of Irian Jaya collected in 1938, and three additional specimens collected by the 1938-39 Archbold Expedition 190 km south-west of the type locality (Parker, 1940; Zweifel, 1979). Based on colour pattern variation and morphology, *L. cheesmanae* appears to be closely related to *L. longiceps* (Parker, 1940). *Lipinia venemai*, described by Brongersma (1953), is known only from two

TABLE 1: Summary of genetic distance values. Uncorrected genetic distances above the diagonal, HKY'85 corrected distances below the diagonal (Hasegawa et al., 1985).

	1	2	3	4	5	6
1 <i>Sphenomorphus leptofasciatus</i>	-	0.10110	0.07802	0.09070	0.10677	0.09480
2 <i>Lipinia rouxi</i>	0.10939	-	0.10519	0.06913	0.09091	0.07305
3 <i>L. leptosoma</i>	0.08309	0.11424	-	0.08903	0.10805	0.09890
4 <i>L. pulchra</i>	0.09746	0.07303	0.09544	-	0.06035	0.06665
5 <i>L. longiceps</i>	0.11611	0.09783	0.11818	0.06329	-	0.07310
6 <i>L. noctua</i>	0.10218	0.07734	0.10716	0.07041	0.07779	-

specimens, the male holotype from Ajamaroe, and female paratype from Djidmaoe, both from the Vogelkop Peninsula of Irian Jaya. Although the specific status of *L. venemai* was upheld by Zweifel (1979) the relationship of this species with the other New Guinean *Lipinia* is undetermined (Zweifel, 1979). *Lipinia miota* was described by Boulenger (1895) from Fergusson Island off the east coast of New Guinea, but Zweifel (1979) synonymized it with *Lipinia noctua*. Given the specific status of *L. rouxi*, which was similarly synonymized with *L. noctua*, and strong morphological conservatism in this group (Austin, 1995), it remains unclear as to whether *L. miota* should be recognized as a distinct species; further molecular work should clarify this issue.

Additionally, at the present time specimens from the large Philippine radiation were not included. Unfortunately many of the Philippine species are also known from a small number of specimens or have very limited ranges (Brown and Alcalá, 1980). Inclusion of these taxa along with other potentially closely related taxa such as *Paralipinia* in future analyses will provide the final samples necessary to answer the question of the biogeographic origins of *Lipinia*. Unfortunately, *Paralipinia* is known only from a single specimen and the habitat of the type locality in Vietnam has recently been severely degraded (I. S. Darevsky, pers. comm.). The secretive arboreal behaviour and patchy distribution of most species of *Lipinia*, however, probably make them appear to be less common than they actually are. *Lipinia macrotympanum*, known only from the holotype described by Stoliczka (1873), was recently rediscovered in the Nicobar Islands over one century after its original description (Das, 1997). *Lipinia rouxi* was only known from fifteen specimens until Austin (1995) collected an additional twenty specimens. Given the remote and densely forested areas involved, it is therefore quite possible that additional populations of previously described species will be discovered along with species new to science for future phylogenetic analyses.

The biogeography of the herpetofauna of south-east Asia and Papua is complex, but recent

systematic work based on morphology and molecules, and a improved understanding of the heterogeneous tectonic history of this region, has provided greater insight into the evolution of this highly diverse reptile and amphibian fauna. The origins of the genus *Lipinia* are unclear as this genus has two centres of abundance, with one area (Philippines) being closely associated with south-east Asia, and the other (New Guinea) having a mixture of several different faunal histories. The variegated Papuan herpetofauna has a high degree of endemics and includes some members that have a south-east Asia origin, others with an Australian origin, and other faunal elements that appear to be of ancient Gondwanan origin. The biogeographic origin and phylogenetic affinities of *Lipinia* are unclear, but the data presented in this study, although somewhat limited, provide some suggestion that the Papuan *Lipinia* are monophyletic and that either island or mainland south-east Asia, rather than New Guinea, may host *Lipinia*'s closest relatives. Indeed, *Paralipinia* from Vietnam, may be the only surviving relative to *Lipinia*. Further morphological and molecular work is clearly necessary to fully understand the biogeographic processes that have been responsible for the current distributions and phylogenetic relationships of *Lipinia*.

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APPENDIX 1: Three hundred and fifty base-pair sequence from the mitochondrial 12S rRNA gene and three hundred and sixty one base-pair sequence for the nuclear *c-mos* gene for six taxa. Dots indicate a match with the first taxon (outgroup), dashes indicate gaps.

12S:

<i>S. leptofasciatus</i>	ATAGTACTAACAACAACACCATCCGCCAGAGAACTACAAGCGAAAAGCTTG
<i>L. rouxi</i>	...- .T.....T.AT.....A.
<i>L. leptosoma</i>	...A.....TT.....A.
<i>L. pulchra</i>	...- .T...T...C...AT.....A.
<i>L. longiceps</i>	...- .TT...T...T...T.....A.
<i>L. noctua</i>	...- .TT...T.....-T.....G.....A.

<i>S. leptofasciatus</i>	AAACTCCAAGGACTTGGCGGTGCTTCAAACCAACCTAGAGGAGCCTGTCC
<i>L. rouxi</i>
<i>L. leptosoma</i>A.....T.....
<i>L. pulchra</i>
<i>L. longiceps</i>T.....
<i>L. noctua</i>T.....

<i>S. leptofasciatus</i>	TATAATCGATACTCCACGTTTACCTCACCGCTCCTTGAAATTCAGCCTA
<i>L. rouxi</i>AA.....T.CTT...CT.AC.....
<i>L. leptosoma</i>A.....A...C...T...A.CA...A.CC.AC.....
<i>L. pulchra</i>C.....C...T...C.C.T.A.CCC-C.....
<i>L. longiceps</i>T...C.CG...A.CC.AC.....
<i>L. noctua</i>C.....CGCA...A.TC.AC.....

<i>S. leptofasciatus</i>	TATACCGCCGTCGCCAGCCTACCTTGTGAAAGAAACAAAGTGAGCAAAAT
<i>L. rouxi</i>T.....A.....GA.....AG.....
<i>L. leptosoma</i>TC...C.A.....G.....
<i>L. pulchra</i>T.....A.....AGA.....C
<i>L. longiceps</i>T.....C.....G.....A.....C
<i>L. noctua</i>T.....A.....G.....A.....

<i>S. leptofasciatus</i>	AGTTA-ACAACCTAGTACGTCAGGTCAAGGTGTAGCACACGAA-GCGGTAG
<i>L. rouxi</i>-T.....AC.....T.GGGAG.-A..
<i>L. leptosoma</i>-.....A.....A...G-.T....
<i>L. pulchra</i>-T.....AA.....T.GGG.G..C..
<i>L. longiceps</i>	.AC.-.T..T..AA.....T.CGG.G.-C..
<i>L. noctua</i>C.....AC.....T.TGTCG.A-..

<i>S. leptofasciatus</i>	AGATGGGCTACATTTTTACAAAGAAAAACACGAATAGCACGTTGAAATC
<i>L. rouxi</i>C.-.C.ATG..C.....A..T.C.....CA
<i>L. leptosoma</i>T..C.....C..TGT.C.....CA
<i>L. pulchra</i>C.-.--AC...C.T.....ATGT.....CA
<i>L. longiceps</i>CT-..GATG..C.T..AG.C.AA.T.....CA
<i>L. noctua</i>C.-.-.ACG..C.T....C.AT.T.....CA

<i>S. leptofasciatus</i>	CCTGCTCGAAGGTGGATTTAGTAGTAAAATAAAAAAGAAAAATTATTTTA
<i>L. rouxi</i>	.A..T.TA.....GAGT.T.....G.CATC..G.
<i>L. leptosoma</i>	.TCA..T.....G.GT.....C.....
<i>L. pulchra</i>	.A.AT.T.....CG.CC.....G.ATA..G.
<i>L. longiceps</i>	.A.AT.A.....T..GC.....T.C.AT..G.
<i>L. noctua</i>	.G.AT.T....C.....C.G.....CATC..G.

C-mos:

<i>S. leptofasciatus</i>	AAGAACCGGTTGGCATCAAGACAAAGCTTCTGGGCAGAACTAAATGTGGT
<i>L. rouxi</i>C.....C.....A.C
<i>L. leptosoma</i>C.....A.C
<i>L. pulchra</i>CA...C.....C
<i>L. longiceps</i>C...C.....C
<i>L. noctua</i>A.....C...C.....C

<i>S. leptofasciatus</i>	ACGCCTTAGTCATAACAATGTGGTACGTGTAATAGCTGCTAGTGCATGTT
<i>L. rouxi</i>A.....
<i>L. leptosoma</i>G.A.....
<i>L. pulchra</i>C.....
<i>L. longiceps</i>A.....
<i>L. noctua</i>

<i>S. leptofasciatus</i>	CTCCTACCAATCAGAACAGTTTGGGTACCATCATAATGGAATATGTAGGT
<i>L. rouxi</i>
<i>L. leptosoma</i>T.G.....
<i>L. pulchra</i>T.....
<i>L. longiceps</i>T.....T.....
<i>L. noctua</i>A.....

<i>S. leptofasciatus</i>	AACAGCACTTTGCACCATGTTATCTATGGGACAGGATGTACTGTAGCAAA
<i>L. rouxi</i>	...G.....A...A...
<i>L. leptosoma</i>TG.....
<i>L. pulchra</i>	...G.....-----
<i>L. longiceps</i>	..TG.....A..GA...
<i>L. noctua</i>	...G...A.....A.....A...A...

<i>S. leptofasciatus</i>	AAGGAAGGATAATGAGCTTGGTTGTGGCTATGAACCTTTGAGTATAATGC
<i>L. rouxi</i>C.....A.....A.....A.....
<i>L. leptosoma</i>A.....A.....
<i>L. pulchra</i>C.....
<i>L. longiceps</i>CA.....
<i>L. noctua</i>C.....--.....

<i>S. leptofasciatus</i>	AGTCTCTGAGCTACTCATGTGACATTGTGGCAGGCTTGGTCTTTCTCCAT
<i>L. rouxi</i>	.C.....A.G.....
<i>L. leptosoma</i>
<i>L. pulchra</i>
<i>L. longiceps</i>T.....C.....
<i>L. noctua</i>C.....A.....

<i>S. leptofasciatus</i>	TCACAATTAAGTGCATCTGGATTAAACCTGCCAACATATTCATCAC
<i>L. rouxi</i>
<i>L. leptosoma</i>
<i>L. pulchra</i>
<i>L. longiceps</i>
<i>L. noctua</i>

<i>S. leptofasciatus</i>	TGAACAAA
<i>L. rouxi</i>
<i>L. leptosoma</i>
<i>L. pulchra</i>
<i>L. longiceps</i>
<i>L. noctua</i>

HOW TO HISS LOUDLY: ON NARIAL FLARING AND ACOUSTIC AMPLIFICATION IN RUSSELL'S VIPER (*DABOIA RUSSELLII*)

Bruce A. Young

Department of Biology, Lafayette College, Easton, Pennsylvania 18042, U.S.A.
Email: youngab@lafayette.edu
(with five text-figures)

ABSTRACT.- Acoustic analyses of Russell's viper, *Daboia russelii*, revealed that these snakes produce a hiss with a mean amplitude of over 82 dB, well above the intensity of most other snake sounds. The frequency range (mean minimum frequency = 471 Hz; mean maximum frequency = 13,925 Hz) and dominant frequency (mean = 8,201 Hz) are similar to those reported from other snakes. The most prominent morphological specialization found in the respiratory system of *D. russelii* is the expansive external nares, which are a diagnostic feature of this species. To determine if the large nares were responsible for increasing the amplitude of the hiss, polyethylene tubing was inserted into the nasal cavity. Hisses produced with the tubing in place had a similar frequency range but decreased in amplitude by over 12 dB.

KEY WORDS.- *Daboia*, Viperidae, Lepidosauria, defensive behaviour, sound production.

INTRODUCTION

Snakes exhibit a variety of defensive behaviour (reviewed by Mertens, 1946; Carpenter and Ferguson, 1977; Greene, 1988) which can be simplistically divided into two main categories, passive and aggressive. Passive defensive behaviour are those in which the snake attempts to minimize either the interaction with the molestor/predator, or the resulting harm; examples would include fleeing, head hiding, death feigning, and the expulsion of odoriferous material from the cloacal glands. Aggressive defensive behaviour are those in which the snake actively attempts to intimidate the molestor/predator into terminating the interaction; examples would include defensive strikes, hooding, spitting venom, and most forms of sound production. In order for an aggressive defensive behaviour to be effective, two conditions must be met: it must be overt enough to be easily and quickly recognized by its potential target, and it must clearly convey some element of warning or danger (e.g., Klump and Shlater, 1984a, 1984b; Dusenbery, 1992).

A variety of sound production mechanisms have been described in snakes (Gans and

Maderson, 1973; Frankenberg and Werner, 1992; Young, 1997). Several of these involve anatomical specializations of the respiratory system or epithelium (Gans, 1961; Young, 1991; Young and Brown, 1995; Young et al., 1995), while others rely simply on the passage of air through the oral or nasal cavity (Kinney et al., 1998, Young and Lalor, 1998). Ophidian defensive sounds have a simple acoustic structure; in most cases they are characterized by a broad frequency range, and the lack of distinct amplitude modulation, frequency modulation, harmonics, and temporal patterning (Young, 1997). Young (1997, 1998) has argued that while the acoustic properties of snake sounds are effective as general warning signals; they probably do not convey enough information to function in intraspecific communication (e.g., Blumstein and Armitage, 1997).

Although the broad frequency range of most ophidian defensive sounds may convey warning or danger to a predator/harasser, not all of these sounds are overt. The cloacal pops produced by *Micruroides euryxanthus* have an amplitude of only 50 dB, making them quieter than normal conversation. With the possible exception of the

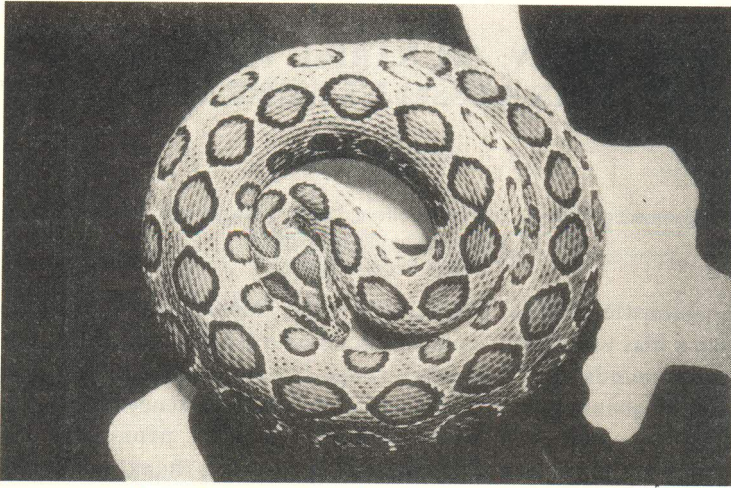


FIGURE 1: Dorsal view of a 60 cm *Daboia russelii* showing the typical defensive posture, note the extensive inflation of the body.

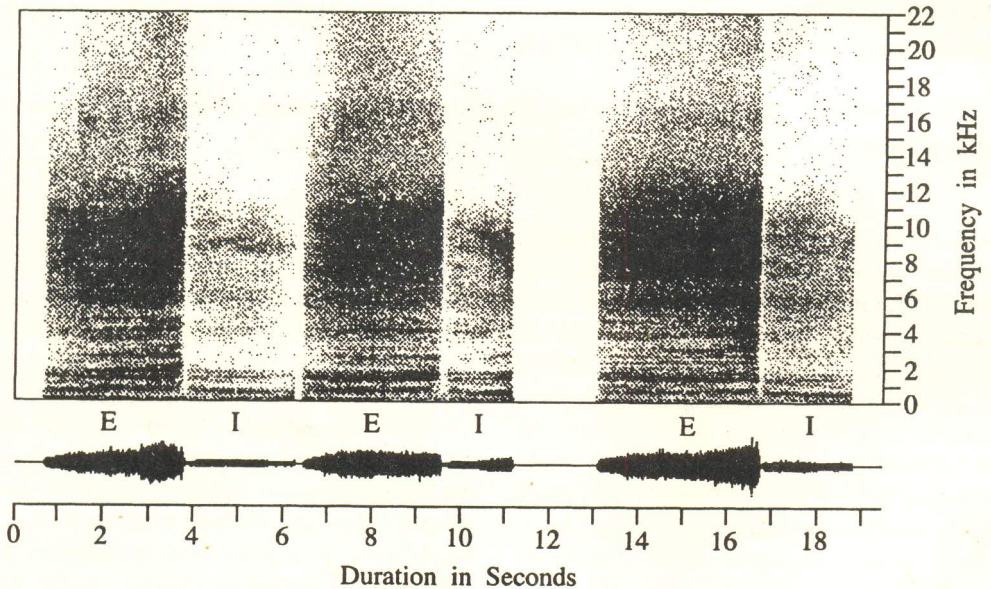


FIGURE 2: Sonogram and amplitude curve for a 20 second segment of defensive sound production from *Daboia russelii* showing the quadruphasic pattern of exhalation (E), a short pause, inhalation (I), then a longer more variable pause. Note the difference in amplitude between the exhalatory and inhalatory sounds, and the broad frequency range of the exhalatory sound.

epiglottal keel in *Pituophis* (Martin and Huey, 1971; Young et al., 1995) there is no evidence of anatomical specializations associated with acoustic amplification in snakes.

Russell's viper, *Daboia russelii*, is one of the most common snakes in southern Asia (Smith, 1943; Wüster, 1998). It is generally described as a rather nervous snake that is prone to defensive

behaviour and strike- accounts of the defensive behaviour normally make reference to its unusually loud hisses (Wall, 1921; Smith, 1943; Whitaker, 1978; Murthy, 1986; Wüster, 1998). Since *D. russelii* is not particularly large for a viper (adult SVL of 100-120 cm; Wüster, 1998), it seems unlikely that this acoustic amplification results purely from increased airflow. The pur-

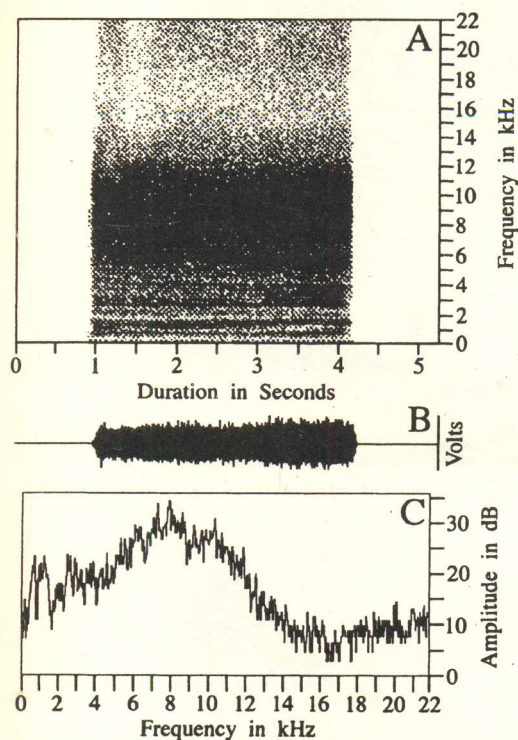


FIGURE 3: Analysis of a typical exhalatory hiss in *Daboia russelii*. A- sonogram; B- amplitude voltage tracing of the 3.2 second hiss; C- Power spectrum analysis of the same hiss. Note the broad frequency span and the absence of frequency modulation, amplitude modulation, or harmonics.

pose of the present contribution is to examine the morphological basis of acoustic amplification in *D. russelii*.

MATERIALS AND METHODS

Morphology.- Specimens of *Daboia russelii* from the author's private collection were dissected to examine the larynx and lower respiratory tract. In one specimen the anterior portion of the skull was removed and bisected parasagittally. One half of the snout region was decalcified in Cal-Ex (Fisher) for 18 days, dehydrated through an ethanol series, cleared in Hemo-De (Fisher), and imbedded in paraffin. Sections were cut (at 10 μ m) just oblique to the transverse plane in order to maximize sections through both the external naris and nasal vestibulum. Complete serial sections of the nasal

passageway were cut. Mounted sections were stained with either Hematoxylin and Eosin (Humason, 1972) or a modified version of Van Gieson's stain (Grande and Young, 1997).

Acoustics.- One group of 12 *Daboia russelii* (mean SVL = 100 cm, range = 60-121, s.d. = 16.2) was analyzed at the Centre for Herpetology, India. Each specimen was placed individually in the centre of a large quiet room and its defensive behaviour evoked by the investigator. The amplitude of the defensive hisses were determined using a 840029 Digital Sound Meter (SPER Scientific) positioned approximately 30 cm from the animal's head. The defensive hisses were recorded using a Fostex X-18 recorder (frequency response 50-12,000 Hz) and an ND 757B (ElectraVoice) microphone (frequency response 50-22,000 Hz) located 40 cm from the head of the specimen. Multiple defensive sounds were analyzed from each specimen. A second group of three *D. russelii* (mean snout-vent length 65 cm, range 60-70 cm), kindly provided by Jim Harrison of the Kentucky Reptile Museum, were maintained on a 12:12 light cycle, water ad libitum, and a temperature range of 27-29.7°C. The specimens were placed individually in a large quiet room and their defensive behaviour evoked. Amplitude of the defensive sounds were determined as described above; the defensive sounds were recorded using an ND 757B (ElectraVoice) microphone (frequency response 50-22,000 Hz) positioned 40 cm from the snake's head. The microphone was coupled to a P511 amplifier (GRASS), an Instrunet Analog/Digital converter (GW Instruments), and a Power Macintosh 6400 (Apple Computer).

Acoustic analyses were conducted using the SoundScope software package (GW Instruments) and the WLFDAF 1.0 (Zola Technologies, Atlanta, GA) digital filtration software. Sonogram and power spectrum analyses (with a sampling rate of 44.1 kHz, a Fast Fourier Transformation (FFT) using 2048 points, and a 59 Hz filter) were used to identify frequency and amplitude modulation, harmonics, and to determine the minimum, dominant, and maximum frequencies. The minimum and maximum frequencies were defined based on amplitude decrease from

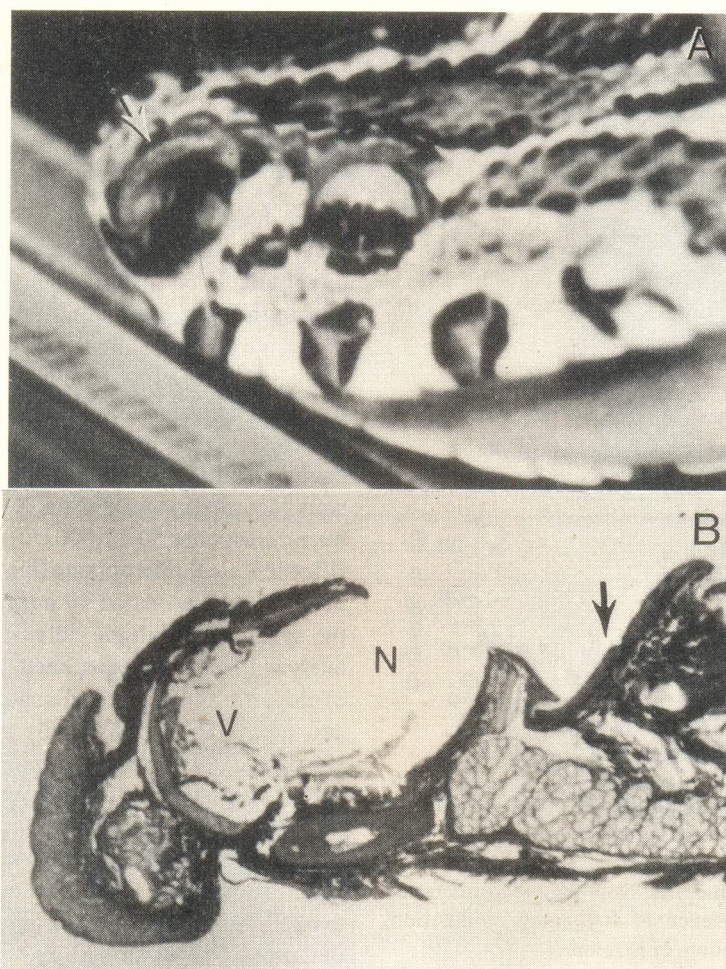


FIGURE 4: A- Lateral view of the head of a 70 cm live specimen of *Daboia russelii* showing the large caudodorsally directed external naris (arrow) of this species. B- oblique section through the nasal vestibulum (V) and external naris (N) of *D. russelii* showing the large diameter of these chambers and the continuity with the lateral surface of the head (arrow).

the dominant frequency. Acoustic limitations in the equipment precluded determining maximum frequencies from the specimens examined at the Centre for Herpetology.

Manipulation of the naris.- After a series of defensive sounds was recorded, the specimens at the Centre for Herpetology were manually restrained and their external nares occluded with a quantity of cotton wadding held in place by surgical tape. After observing the behavioural impact of this manipulation, the cotton plugs were removed and the specimens released to the wild.

After recording a series of defensive sounds from the specimens examined in the author's

laboratory, the snakes were restrained and a segment of polyethylene tubing inserted into each external naris. The tubing (external diameter 2.8 mm) fitted snugly into the nasal vestibulum, its internal diameter (1.7 mm) was large enough to permit unrestricted airflow during ventilation and sound production. The tubing protruded approximately 5 mm beyond the scalation defining the external nares.

RESULTS

General behaviour.- All of the specimens examined exhibited pronounced defensive behaviour. With the slightest provocation the animals

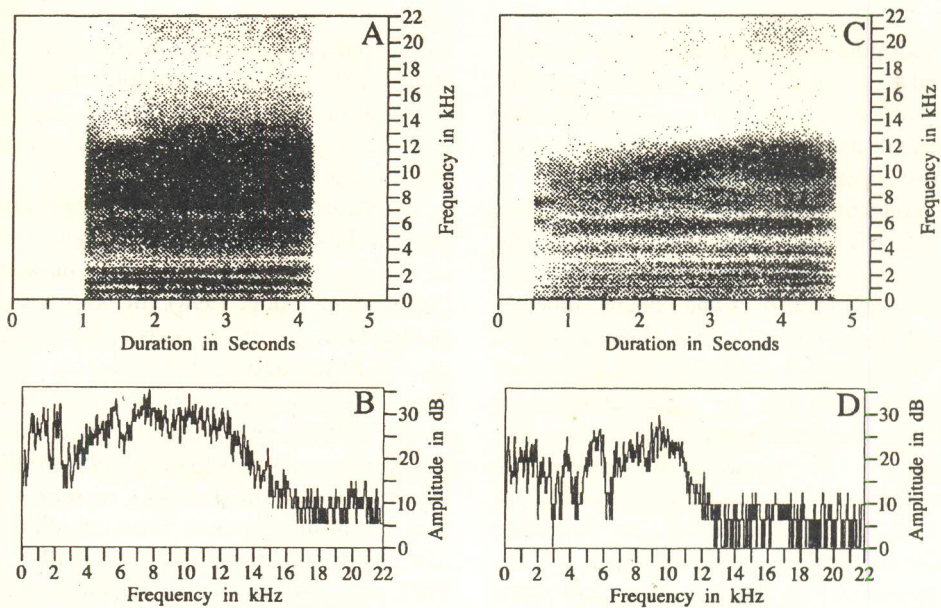


FIGURE 5: Analysis of the exhalatory hiss from a 70 cm specimen of *Daboia russelii* before (A & B) and after (C & D) the insertion of a polyethylene tube into the nasal vestibulum. A- Sonogram, B- Power spectrum of the same hiss produced prior to the insertion of the polyethylene tube; C- Sonogram, D- Power spectrum of the same hiss as in (C) produced after the insertion of the polyethylene tube into the nasal vestibulum. Note the decrease in amplitude between A and C (indicated by colour intensity), but the general similarity in the distribution of acoustic energy.

adopted a characteristic coiled pattern with the head held between two body segments; frequently, the entire head was covered by the body segments (Fig. 1). From this position the snakes produced repeated, nearly continuous, hisses with the mouth closed. The alterations of lung volume which produce the airflow associated with sound production are evidenced by marked expansion and contraction along almost the entire length of the snake's body. While showing little inclination toward locomotion during this defensive behaviour, almost every specimen attempted multiple defensive strikes.

Acoustics.- The defensive sounds of *Daboia russelii* had a distinctive quadraphasic pattern consisting of an exhalatory sound (hiss), a brief pause, a lower amplitude inhalatory sound, and a second pause (Fig. 2). While the pause between exhalation and inhalation was always short, the other segments of the sound were quite variable. The exhalatory hiss had a mean duration of 3.4 sec, a range of 1.8-5.4 sec, and a standard deviation of 1.1 sec ($n = 15$). The hiss is a high ampli-

tude sound with a mean amplitude of 82.2 dB (RMS, SPL) (range 74.3-91.2, s.d. = 4.2, $n = 15$). The hiss of *D. russelii* has a broad frequency range with a mean minimum frequency of 471 Hz (range 125-1,109, s.d. = 395, $n = 3$), a mean maximum frequency of 13,925 Hz (range 12,075-19,968, s.d. = 1,684, $n = 3$), and a mean dominant frequency of 8,201 Hz (range 7186-10,318, s.d. = 976, $n = 3$; Fig. 3). There was little evidence for amplitude modulation, frequency modulation, harmonics, or temporal patterning within the hiss (Fig. 3). The maximum frequency of the hiss exceeded the frequency response of the equipment used in India; however, the minimum (mean 640 Hz, $n = 12$) and dominant (mean 7,876 Hz, $n = 12$) frequencies from the snakes examined at the Centre for Herpetology were similar to the specimens examined in the author's laboratory.

Morphology.- The respiratory system of *Daboia russelii* has been previously described (George and Varde, 1941; Varde, 1951; George and Shah, 1956; Bergman, 1961); herein only a

brief description will be provided. The vascular lung and air sac of *D. russelii* show no anatomical specializations for sound production; the trachea, despite the presence of an elongate tracheal lung, also appears to serve no special function in sound production. The larynx has a high glottal angle (sensu Young, 1998) and a low epiglottal ridge, but no internal partitions or diverticula. The nasopharyngeal duct and choanal tube are large, while the volume of the choanal zone is small. The distal end of the choanal tube deflects laterally to open into the more lateral nasal vestibulum. The nasal vestibulum is expansive and there is little demarcation between the vestibulum and the large external naris (Fig. 4). The large external naris is directed caudodorsally and is continuous with a well defined depression on the lateral surface of the head (Fig. 4).

Manipulation of the nares.—Occluding the external nares with cotton and surgical tape prevented hissing in *Daboia russelii*. The specimens never switched to open mouth hissing. On occasion the snake was able to generate enough air pressure to dislodge a portion of the occluding plug and produce a soft hiss accompanied by visible movement of the surgical tape. Insertion of a polyethylene tubing into the distal part of the nasal vestibulum had no significant impact on the minimum and dominant frequencies of the hiss, but did significantly (Student's *t*, $P < 0.05$) lower the maximum frequency (Fig. 5). The presence of a tube within the nasal vestibulum produced a significant (Student's *t*, $P < 0.05$) decrease in mean amplitude of almost 12 dB (from $\bar{x} = 83.6$ to $\bar{x} = 71.8$ dB).

DISCUSSION

The closed mouth posture maintained by *Daboia russelii* during hissing, coupled with the disruption of hissing produced by occluding the nares, indicates that the exhalatory airflow associated with hissing passes through the nasal passageway. A similar conclusion was reached by Wall (1921) who described how the hiss of *Vipera* (= *Daboia*) *russelii* was changed following the insertion of cotton into the nostrils. Like several other snakes (Kinney et al., 1997; Young and

Lalor, 1998) and monitors (Young et al., 1998), *D. russelii* appears to be an obligate nasal exhaler in that at no time, even following nasal occlusion, did the specimens switch to sound production through the oral cavity.

The quadruphasic pattern observed in *Daboia russelii* has been previously described for *Heterodon platyrhinos*, another nasal hisser (Young and Lalor, 1998). In both cases, this quadruphasic pattern appears to be a direct reflection of the basic ophidian ventilatory cycle (Stinner, 1982). The frequency range of the hiss produced by *D. russelii* is slightly wider than that of a typical snake hiss (Young, 1991, 1997), but the amplitude of the hiss of *D. russelii* is higher than that of most snakes. Most ophidian defensive sounds range between 50 and 70 dB (Young, 1997, pers. obs), well below the mean amplitude of 82.2 dB observed in *D. russelii*.

Other large snakes, including vipers, do not generally produce as loud a hiss as *Daboia russelii* (Young, pers. obs). This increased amplitude is not due simply to airflow through the nasal passageway, since other nasal hissers produce sounds of lower amplitude (Kinney et al., 1998; Young and Lalor, 1998). The lung of *D. russelii* is extensive, but is similar to those of other vipers (Wallach, 1998). The trachea and larynx are similar to those of other snakes (Wallach, 1998; Young, 1991, 1998) and do not show any specializations associated with sound amplification. The nasal passageway, with the exception of the external nostril, also shows no distinct morphological specializations.

The large nostril of *Daboia russelii* has been frequently noted and is often cited in descriptions of this species (e.g., Wall, 1921; Smith, 1943; Wüster, 1998). The enlarged external nares, as well as the configuration of the adjacent surface of the head, represent a continuous expansion from the nasal vestibulum (Fig. 4). All else being equal, the intensity (*I*) of a sound is proportional to the square of the pressure (*P*) and inversely proportional to the acoustic impedance (*Z*), that is, $I = P^2/Z$ (Bradbury and Verkamp, 1998). The narial expansion characteristic of *D. russelii* appears to function like the flared end of horn (Fletcher and Rossing, 1991) in reducing

the acoustic impedance thereby increasing the intensity of the sound. Increasing lung size could serve to increase pressure (P), but the morphology of *D. russelii*, coupled with the apparent absence of unusually loud hisses in other vipers, suggests that this is not a major factor.

The hypothesis that the nostril of *Daboia russelii* functions like the flare of a trumpet to increase the intensity of the hiss, is very amenable to testing. The acoustics of the trumpet flare can be modified by the insertion of a mute, which reduces the intensity of the sound and causes some shifts in frequency (Fletcher and Rossing, 1991). The polyethylene tube inserted into the nostril of *D. russelii* was intended to function as an open mute (viz., one that allows airflow through its centre). The significant decrease in acoustic intensity, and change in frequency span (Fig. 5) are taken as evidence that the inserted tube functioned like a mute. Since the tube was nearly the same diameter as the nasal vestibulum, the only direct impact of the presence of the tube was to eliminate the flaring of the external nares.

Flaring of the external nares would appear to be a relatively simple means of increasing the intensity of defensive sounds. This mechanism may be impossible for aquatic or fossorial species which often have some form of valvular nostril (Kathariner, 1900; Parsons, 1970), and may lead to increased evaporative water loss in desert forms. The expansive nostrils of *Daboia russelii* represent a specialization for increasing the conspicuousness, and thus presumably the effectiveness, of the defensive sound.

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This project would have been impossible without the kindness and cooperation of the staff of the Centre for Herpetology, Madras Crocodile Bank Trust. Special thanks to Jim Harrison and the Kentucky Reptile Museum for the loan of their animals, and to C. Marsit and K. Meltzer for their comments on an earlier version of this manuscript.

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HERPETOFAUNA OF THE CHATTHIN WILDLIFE SANCTUARY, NORTH-CENTRAL MYANMAR WITH PRELIMINARY OBSERVATIONS OF THEIR NATURAL HISTORY

George R. Zug¹, Htun Win², Thin Thin², Than Zaw Min², Win Zaw Lhon², and Kyaw Kyaw²

¹Division of Amphibians & Reptiles, National Museum of Natural History,
Washington, D.C. 20560, U.S.A.
Email: zug.george @nmnh.si.edu.

²Chatthin Wildlife Sanctuary, c/o Nature and Wildlife Conservation Division,
Forest Department, West Gyogone, Insein, Yangon Myanmar.
(with two text-figures)

ABSTRACT.- Sixteen species of amphibians and 34 species of reptiles comprise the herpetofauna of a dry deciduous dipterocarp forest and adjacent farmlands of a wildlife preserve in north-central Myanmar. Numerically, several species of frogs (e.g., *Rana limnocharis*, *Rana rugulosa*, *Microhyla* sp.) are the most abundant components of the Chatthin herpetofauna, and no species of reptile approaches their abundance or density. The area has a strong seasonal shift between wet (monsoon) and dry, and all species show distinct patterns of seasonal activity and associated abundance, no less so for any reptilian species.

KEY WORDS.- Amphibia, Reptilia, natural history, size of adults, Burma, Myanmar.

INTRODUCTION

The Chatthin Wildlife Sanctuary (23° 34.46'N; 95° 44.26'E) is a 268.2 km² nature reserve approximately 160 km north-west of Mandalay, in central Myanmar (Fig. 1). The sanctuary was formed by the British Territorial Government of Burma in 1941 by combining two adjacent forest reserves and unassigned forest (Salter and Sayer, 1983). It was created mainly as a preserve for the thamin or Eld's deer (*Cervus eldi*), but the Japanese supported invasion in 1942, the subsequent war years, and the early years of independence offered little opportunity to protect the thamin or other animal and plant species. Nonetheless, the reserve was recognized locally and received some attention by the Myanmar Forestry Department. When the wildlife division was established within the forestry department in 1986, the division established a station (San Myaung Camp) near the town of Chatthin, and they began a programme of protection and regular patrols.

Chatthin W. S. (ca. 200 m above msl) is mainly a secondary growth indaing forest with several seasonally flooded areas of open grassland (lwin) and a seasonally large lake near the

north-western edge of the W. S. The W. S. also includes three small villages and their associated farmland. The eastern, northern, and western perimeter borders mainly rice paddies, the southern abuts secondary-growth forest. The indaing is deciduous dipterocarp forest dominated by the In (*Dipterocarpus tuberculatus*); about two-thirds of the forest is low indaing with tree tops at 8-10 m, the remainder high indaing reaching 10-15 m. In both, the canopy is open, 30-70%, and the forest floor has a mixture of forbs and grass or mainly grass, never dense beneath the canopy. The shrub layer ranges from sparse to moderate with a variety of other low shrubs and trees and In sprouting from root stocks.

In 1994, the Smithsonian's National Zoological Park/Conservation and Research Center began a collaborative research programme with the Myanmar Nature and Wildlife Conservation Division on the ecology of the thamin. Subsequently, they initiated a bird census programme in late 1995, and in July 1997, we began a herpetofaunal inventory and monitoring program. The programme has three components that

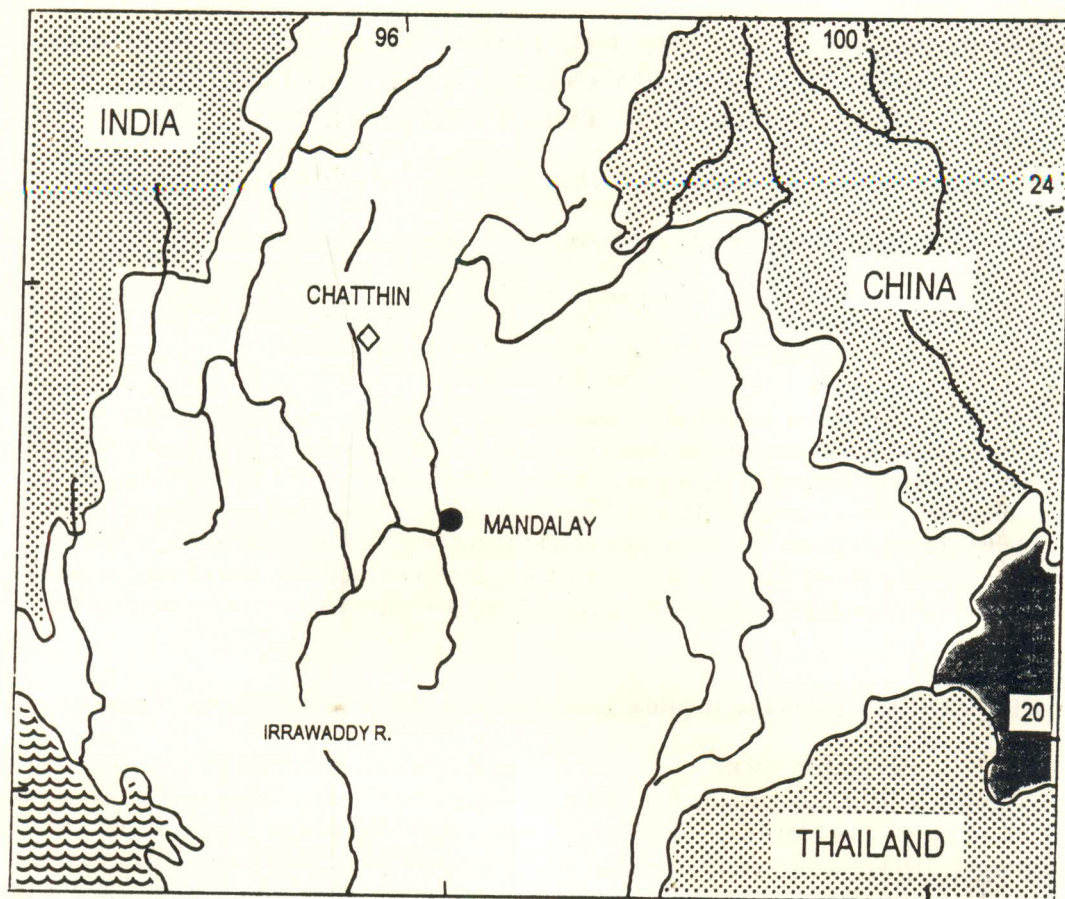


FIGURE 1: Location of the Chatthin Wildlife Sanctuary in north-central Myanmar.

operate weekly or monthly year around. Although we do not yet know all of the amphibians and reptiles of the sanctuary, we believe that it is appropriate to provide a preliminary list of the herpetofauna and some of our observations on their natural history from our first year of monitoring. This goal is important, because aside from Dowling and Jenner's (1987) snake checklist, the most recent published observations on the Myanmar herpetofauna derive from the time of British administration (e.g., Shreve, 1940; Smith, 1940; 1943).

CHATTHIN HERPETOFAUNA

The Chatthin fauna contains at least 16 species of frogs, two turtles, 12 lizards, and 20 snakes (Table 1). The following accounts provide data on adult snout-vent length (SVL, separately for

adult females and males, and sample sizes; unless noted otherwise, all measurements were taken pre-preservation), an estimate of abundance (abundant, common, uncommon, rare), main habitat and microhabitat occurrence, and miscellaneous observations on the biology of the species. Sex and maturity were determined by dissection and examination of gonads in reptiles, examination on gonads and/or presence of functional vocal sacs in frogs. All species reported here are represented by voucher specimens in the Chatthin W.S. Collection (ChWS) and/or National Museum of Natural History, Smithsonian Institution (USNM); see Appendix I.

FROGS

Bufo melanostictus (Bufonidae). 99-113 mm, 74-101 mm SVL, $n = 3$ females, 2 males. Un-

calls on ground. It is arboreal, occurring in fence rows and isolated trees in the farmland and forest; diurnal "rain-calls" demonstrate its presence to 6-8 m height in densely foliated trees.

Polypedates leucomastyx (Rhacophoridae). 77 mm, 48-60 mm SVL, $n = 1, 12$. Uncommon; this species breeds with the earliest rains (May-early June) of the monsoon and is seen only sporadically thereafter during the monsoon. Males occasionally call from the ground, but more frequently from shrubs near temporary forest pools, usually < 2 m from ground.

Glyphoglossus molossus (Microhylidae). 86 mm, 63-77 mm SVL, $n = 1, 6$. Uncommon; juveniles and adults have been found in our forest floor surveys and in breeding aggregations. Body form and the large heel spade suggest a fossorial life-style. Breeding occurs in the early monsoon in deep, temporary forest pools. Males call from a floating posture, usually clustered in the middle of the pool. They are extremely wary and sink with the slightest disturbance. The size disparity between the sexes prevents typical amplexus, and the male is broadly glued to the female's back.

Kalophrynus interlineatus (Microhylidae). 39-44 mm SVL, $n = 4, 0$. Rare; this species has been found only as single individuals within the forest on the forest floor.

Kaloula pulchra (Microhylidae). 67 mm, 61-70 mm SVL, $n = 1, 3$. Uncommon; it is found predominantly in the forest, and all breeding males have been found in forest or forest-edge pools, although it is a known resident of garden and landscaped sites in villages and towns. Breeding occurs in the early monsoon with the males calling in the water at the edge of pools.

Microhyla ornata (Microhylidae). 20-27 mm, 20-25 mm SVL, $n = 7, 11$. Common; it occurs in forest and farmland. Its breeding season extends from early through mid-monsoon with peak chorusing activity in the latter half of this period. Males call from the ground and typically partially or completely hidden under vegetation.

Microhyla sp. (Microhylidae). 16-18 mm, 14-17 mm SVL, $n = 6, 22$. Abundant; most specimens derive from breeding choruses which occur in farmland or at forest edge, although a few

individuals have been found in forest litter surveys. Chorus activity begins in early monsoon and continues throughout the monsoon. The tiny males call from land and always beneath vegetation.

Occidozyga lima (Ranidae). 24-40 mm, 22-30 mm SVL, $n = 6, 33$. Abundant; it occurs in forest and farmland. It is a most common paddy frog and regularly found in ditches and puddles. Although it moves overland, it is seldom far from water. Chorusing and breeding occurs from early to late monsoon. Males call mainly from a floating posture and occasionally sitting on vegetation in the water.

Rana lateralis (Ranidae). 55-64 mm SVL, $n = 0, 10$. Uncommon; this species has been found only as single individuals within the forest or at forest edge. Adult males have been found most frequently in early monsoon, but we have not found a breeding aggregation or even a single calling male.

Rana limnocharis group. Two species of the *R. limnocharis* group occur. Both species are abundant, and the larger species matches the Thai populations identified as this species. The small species initially were mistaken for juveniles, but calling males are common.

Rana limnocharis/large (Ranidae). 47-67 mm, 39-52 mm SVL, $n = 27, 34$. Abundant; this species occurs throughout the forest and farmlands, usually associated with water although it is occasionally seen, both during the day and night, foraging 100 m or more from the nearest water. Males call year around when conditions are wet, and even sporadically during the day; although main breeding choruses are nocturnal, usually beginning several hours after sunset and continuing into the early morning. Males call from the water's edge, sitting in the water or on land. *R. limnocharis* is wary and escapes by a series of leaps away from the intruder. This species and *R. rugulosa* are collected by the locals and are sold as "finger-food" at the Chatthin village market.

Rana limnocharis/small (Ranidae). 30-39 mm, 24-29 mm SVL, $n = 6, 18$. Common; this species is a paddy frog and otherwise has been seen only at the forest edge. Choruses appear

once the monsoon rain have flooded the paddies with persistent water; although an occasional male is heard nearly year around. Males call from land, at the edge of the water to 1 m away.

Rana macrodactyla (Ranidae). Rare; only two juveniles (34.5, 25.2 mm SVL, July & November, respectively) have been captured. The occurrence of these juveniles indicates that breeding occurs near the Sanctuary's headquarters, although we have not seen a breeding aggregation or an adult.

Rana rugulosa (Ranidae). 70-107 mm, 49-54 mm SVL, $n = 8, 9$. Common; *R. rugulosa* is a wetlands species, always in association with water from the rice paddies of the farmlands to temporary pools in the forest and the flooded grasslands (lwin) within the forest. In small pools of water, this species commonly escapes by hopping out of the water and hiding in the adjacent vegetation or leaf litter. Choruses begin prior to the monsoon rains and continue through the entire monsoon, although reproduction appears to be early to mid-monsoon (May-August) based on the occurrence of gravid females. Males call sitting in the water, either at the edge or in shallow areas.

Rana tigerina (Ranidae). 83 mm SVL, $n = 0, 1$. Rare; a single adult male was found in the low indaing beneath leaf litter in the late dry season (mid-May). A darkening of the throat over the vocal sac areas suggest it was approaching breeding condition.

Tomopterna breviceps (Ranidae). 53-61 mm, 50-54 mm SVL, $n = 5, 9$. Common but strongly seasonal; this frog breeds with the first monsoon rains and then largely disappears with only an occasional individual calling to mid-monsoon. The well-developed heel spade denotes at least a semifossorial life-style, and our forest litter surveys indicate that it is a denizen of the forest.

TURTLES

Indotestudo elongata (Testudinidae). Uncommon; this species has long been collected by villagers for food. It is a deciduous forest species. A single juvenile was found in May 1998; all other records derive from carapaces found near villages. This juvenile (77 mm CL; photo-

graphed and released) was hiding at midday beside a termite mound in the high indaing. It possessed a single growth annulus on each scute suggesting that it was in its second growth season or would soon renew its growth in the forthcoming monsoon.

Lissemys scutata (Trionychidae). Uncommon; we obtained two individuals (100, 102 mm CL/preserved, presumed juveniles) in July 1997. It occurs year around in permanent streams and the deep pools in the forest chaungs (streambeds) that persist through the dry season. Local farmers report that it aestivates in burrows adjacent to chaungs or ponds during the dry season. One of our vouchers was found in a roadside puddle near a monsoon-filled stream; the other was purchased from a local farmer, both in mid-monsoon. This species is also collected by villagers for food.

LIZARDS

Calotes mystaceus (Agamidae). 104-112 mm, 134-158 mm SVL, $n = 2, 2$ possible males. Uncommon; this species occurs mainly in farmlands and fence rows and is rarely seen in the forest. Although arboreal, one individual was found beneath leaf litter in January, suggesting terrestrial hibernation during the cool-dry season. One of the females had four oviducal eggs, each approximately 18 mm in maximum length.

Calotes versicolor (Agamidae) 63-80 mm, 80 mm SVL, $n = 5, 1$. Uncommon; although this species is a forest to forest edge and fencerow species, it is not abundant in the forest. Our various census protocols indicate less than one individual per hectare. *C. versicolor* is semiarboreal, appearing to forage on the ground, but usually escaping to and up trees. At night, it is found sleeping on trees and shrubs near the end of the branches and from 1-4 m above the ground. Adult females collected May-August had either mid-vitellogenic follicles or oviducal eggs (4-5; approximately 10-14 mm maximum length). Two juveniles with yolk-sac scars were collected in late July, suggesting a late June to mid-July hatching.

Leiolepis peguensis (Agamidae). Uncommon; we have captured only two individuals

(74.9, 110.7 mm SVL, the larger one is an immature female). *L. peguensis* is largely inactive for about half of the year. It is restricted to elevated, well-drained, open sandy areas in the forest. Individuals live in burrows and are active during the dry season from March through June, "requiring" hot sunny weather. It is most visible when daily temperatures exceed 30°C and is seen outside of its burrows even in midday when temperatures approach 40°C. Most often, it escapes by running to its burrow, but if cutoff from the burrow, it may climb a tree. In the monsoon season, it closes its burrow, presumably for hibernation. We suspect that only one lizard occupies a burrow system, which consists of a "main" entrance and an accessory or escape exit. They have been observed eating plants and animals, including *Brassa* grass and termites.

Gekko gekko (Gekkonidae). 161-162 mm SVL, $n = 0, 2$. Uncommon; it occurs most frequently as a commensal in buildings but also lives in the forest. Usually, only one individual occurs in a building or a set of adjacent buildings. When two individuals are present, one of them is smaller, perhaps a female and male sharing overlapping territories. *G. gekko*, presumably males, call irregularly throughout the day and night from February into June. This gecko stays high in buildings and trees. It eats large insects, mice, and perhaps other geckos, such as *Hemidactylus frenatus*, although we have observed no chases or captures of smaller geckos. Chatthin individuals move about their "territories" throughout the night. One individual occupied three adjacent buildings and moved among them on an irregular pattern, although it did not change its hunting building during a single foraging night.

Hemidactylus bowringi (Gekkonidae). 43-44 mm, 44-47 mm SVL, $n = 3, 2$. Uncommon; *H. bowringi* is a forest gecko, most commonly found on the forest floor beneath detritus and also at the base of trees and beneath bark of standing dead trees. Our preliminary observations suggest a seasonal activity pattern, being most active during the monsoon; we saw individuals in July-September and January-February. A gravid female (USNM 520557, 44 mm SVL) collected in the forest more than 1 km from hu-

man buildings appears to be a hybrid between *H. bowringi* and *H. frenatus*.

Hemidactylus frenatus (Gekkonidae). 48-56 mm, 53-57 mm SVL, $n = 5, 3$. Common; *H. frenatus* is strictly a human commensal, on buildings or vegetation adjacent to buildings. Although principally a nocturnal lizard, it appears and captures insects from 1-2 hr prior to sunset through the night to about 1 hr after sunrise.

Lygosoma lineolatum (Scincidae). 47-52 mm, 46-51 mm SVL, $n = 8, 3$. Common; this skink is a forest floor inhabitant, occasionally seen foraging above the leaf litter but most frequently found beneath floor litter, seeming exclusively so during the heavy rain periods of the mid-monsoon. Reproductive states show several peculiarities. One specimen is hermaphroditic, possessing testes and a left oviduct. Gravid females occurred only in the late July sample and have either two or three oviducal eggs (7.0-9.3 mm, max. length). The minimum of size of sexually mature females is 47.1 mm SVL, yet three females > 50 were immature.

Mabuya dissimilis (Scincidae). Rare; we have seen only a few individuals of this species and only in July. Both specimens appear immature: the male (49.6 mm SVL/preserved) has moderate-sized testes and small epididymides; the female (72.0 mm SVL) has previtellogenic follicles and unconvoluted oviducts.

Mabuya novemcarinata (Scincidae). 78 mm SVL, $n = 0, 1$. Rare; a single individual has been collected in the sanctuary in August.

Mabuya quadricarinata (Scincidae). 45-46 mm SVL, $n = 0, 2$. Rare; we have seen only two individuals. Both were adult males and were captured in early August in the forest.

Sphenomorphus maculatus (Scincidae). 56 mm, 50-51 mm SVL, $n = 1, 2$. Uncommon; *S. maculatus* is a forest floor species. It has a seasonal activity pattern and is most abundant (= visible) in the dry season, February through mid June, although it has been seen in most months.

Varanus bengalensis (Varanidae). 326 mm SVL/preserved, $n = 0, 0, 1$ not sexed. Rare; few monitors are seen within the forest.

SNAKES

Ahaetulla nasuta (Colubridae). 295 mm SVL, n = 0, 1. Rare; this species has been seen only once near the forest edge in a cluster of trees at 3 m.

Amphiesma stolatum (Colubridae). 340-556 mm SVL, n = 5, 0. Common; *A. stolatum* is the most frequently encountered of the Chatthin snakes. It is seen mainly at the forest edge and in the adjacent farmlands; however, it is also seen in the forest, usually near or in open habitats. A gravid female (533 mm SVL, 6 June 1998) bore 10 oviducal eggs, 21-24 mm maximum length.

Boiga multomaculata (Colubridae). 678 mm SVL, n = 0, 1. Uncommon; this species is a forest species. All specimens have been found on the ground beneath leaf litter or logs.

Boiga ochracea (Colubridae). 666 mm SVL, n = 1, 0. Rare; a single individual was found in the forest beneath leaf litter.

Chrysopelea ornata (Colubridae). 883 mm SVL, n = 0, 1. Uncommon; *C. ornata* is a forest species and an exceptional climber. When disturbed on the ground, it moves to the nearest tree and rapidly ascends whether bark is smooth or rough by concertina locomotion that is performed so rapidly that it appears serpentine. In the trees, it is commonly seen at heights > 4 m and does glide from tree to tree or ground when chased.

Dendrelaphis subocularis (Colubridae). 411-426 mm SVL, n = 0, 2. Rare, this species lives in the forest. Both individuals have large testes and small epididymides; nonetheless, we assume that they are mature. They are dimorphic; one has a dark grey venter except for a white chin and throat, the other has a white venter from chin to posterior third of trunk then gradually becoming grey.

Elaphe radiata (Colubridae). 1336 mm, 1630 mm SVL, n = 0, 1, 1 not sexed. Rare; although this species is likely an inhabitant of farmlands, we have observed it only in the forest.

Lycodon aulicus (Colubridae). 479 mm, 305-324 mm SVL, n = 1, 3. Common; this species occurs in forest and forest-edge habitats. It is a terrestrial species, occurring beneath logs and leaf litter. It is likely a crepuscular or nocturnal species as we have captured specimens around

the camp shortly after sunset. Although *L. aulicus* is principally a terrestrial species, it will attempt to avoid capture by climbing trees using concertina locomotion.

Oligodon cruentatus (Colubridae). 305 mm SVL, n = 0, 1. Uncommon; three individual were captured in the forest.

Oligodon quadrilineatus (Colubridae). 537 mm SVL, n = 0, 1. Uncommon; *O. quadrilineatus* is a forest floor inhabitant and the most abundant (n = 6) of the three Chatthin *Oligodon* sp. It was seen in early morning and late afternoon moving on the surface of the litter, and discovered at other times beneath the leaves and logs. A juvenile female (234 mm SVL) regurgitated two lizard eggs (17 mm maximum length, presumably *Calotes mystaceus* eggs).

Oligodon splendidus (Colubridae). 460 mm, 519 mm SVL, n = 0, 1, 1 not sexed. Rare; this snake is a forest-floor inhabitant.

Ptyas mucosus (Colubridae). 1651 mm SVL, n = 0, 0, 1 not sexed. Rare; we saw a single individual in the forest. This species may be more common in the farmlands surrounding the sanctuary.

Sibynophis collaris (Colubridae). Rare; one juvenile male (161 mm SVL) was captured in the forest.

Cylindrophis ruffus (Cylindrophidae). 270 mm SVL/preserved, n = 0, 0, 1 not sexed. Rare; this species was seen only once, several years ago.

Bungarus fasciatus (Elapidae). 1290 mm SVL, n = 1, 0. Uncommon; all specimens (two juveniles, one adult) were found in the farmlands and at night.

Naja kaouthia (Elapidae). 945 mm SVL, n = 1, 0. Uncommon; all specimens were found in the farmlands, both at day and night

Ramphotyphlops braminus (Typhlopidae). Common; this species is found on the forest floor and beneath floor-debris in the monsoon season. The largest individual captured was 120 mm SVL, but most are less than 90 mm SVL; we have not attempted to determine the size at sexual maturity in our sample.

Daboia russelii (Viperidae). 819-830 mm SVL, n = 0, 2. Rare in the forest, uncommon in

the farmlands. This viper becomes active at twilight.

Trimeresurus erythurus (Viperidae). Rare; this snake is a forest species. Two juveniles (390, 400 mm SVL; late November and early December) were found during the cool dry season, one on the forest floor and the other in a shrub at < 1 m above the ground.

Xenopeltis unicolor (Xenopeltidae). Rare; this species seems to require moist forest soils. Both individuals are immature (ca. 400 mm SVL) and were found in forest litter near the kitchen water-overflow at the sanctuary's headquarters.

DISCUSSION

Our inventory of the Chatthin herpetofauna is only one year old, and we certainly have not en-

countered all species that occur in the sanctuary. However, we are using a variety of survey protocols, thus it seems likely that we now have identified the major herpetofaunal components. The species accumulation curve (Fig. 2) shows that our survey efforts are approaching an asymptote and the total Chatthin herpetofauna is likely $60 \pm$ species.

The herpetofauna seems depauperate, although we have no other Burmese sites with which to compare it. The closest locality that has been thoroughly surveyed (Inger and Colwell, 1977) is the Sakaerat forest reserve in north-eastern Thailand ($14^{\circ} 30'N$; $101^{\circ} 55'E$). Although Sakaerat is at a lower latitude, it shares climatic and floral similarities with a strong seasonal rainfall, also an elevation of about 200 m, and an open deciduous dipterocarp forest with

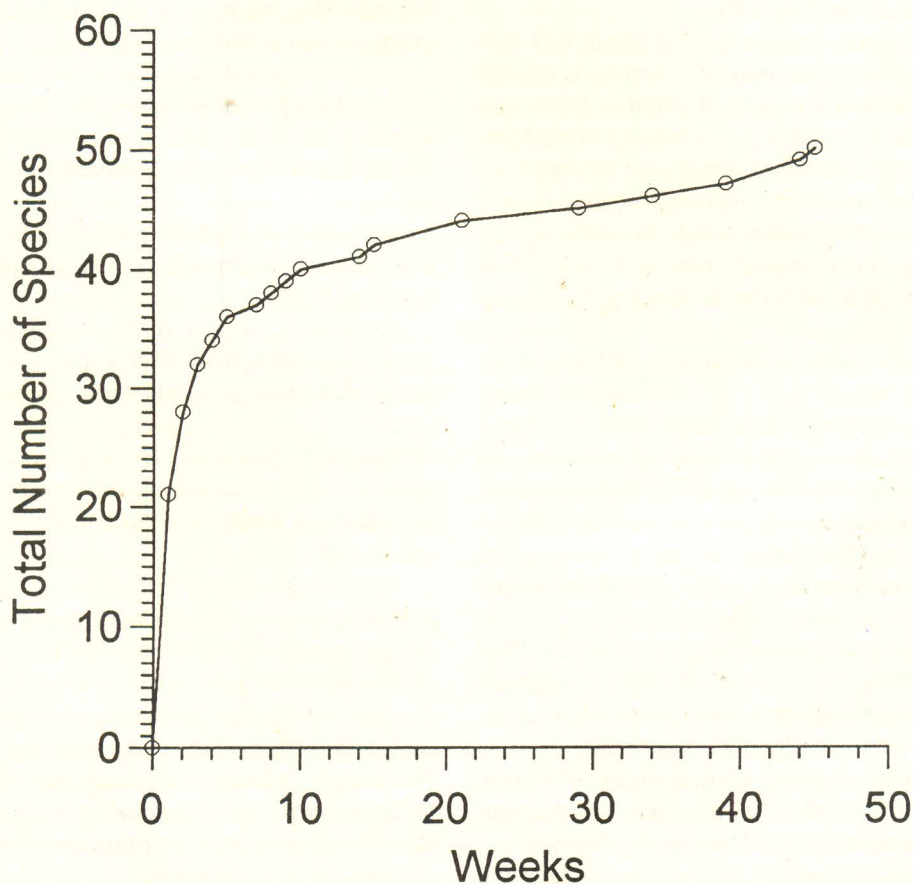


FIGURE 2: Species accumulation curve for the herpetofaunal survey of the Chatthin Wildlife Sanctuary. The survey began on 14 July 1997, and this graph reports our inventory results through 16 June 1998.

adjacent agricultural lands. It also possesses a lowland evergreen forest, but the herpetofauna of that habitat is excluded from the following discussion because no such forest exists near Chatthin. Sakaerat has 24 amphibians (a caecilian, 23 frogs) and 57 reptiles (two turtles, 21 lizards, 35 snakes). With a herpetofauna x 1.5 larger than Chatthin, the impression of a depauperate fauna is supported, but the intensity of sampling at Sakaerat exceeds that performed at Chatthin even though the former sampling occurred only for 11 months.

We are struck more by the similarities of the two faunas than by their differences, considering that the two herpetofaunas are 1,200 km apart and separated by a major mountain range. They share the same species or ecologically-equivalent species. For example, among the frogs, they share ten species (more than half of the known Chatthin anuran fauna); ecological-equivalents would make this number higher. The similarities are at about the same level among the reptiles (e.g., seven shared lizard species and 12 snakes; both more than half the Chatthin faunas). Our ongoing monitoring activities and forest-floor quadrat sampling will allow us to make a more rigorous and statistical comparison of these two faunas in the future.

Such a comparison will also be possible on the relative abundance of the herpetofaunal components. At this time, we are struck by the greater abundance (= visibility) of the anuran fauna in contrast to the reptilian fauna. This abundance is evident in the forest and paddies. The slightest amount of moisture increases the exposed activity of frogs, particularly *Rana limnocharis*, and in the forest, this species is as likely to be observed as any lizard. Indeed, most reptiles are uncommon to rare, and many show a strong seasonality of occurrence. There seems to be an especially low abundance of lizards. Is it possible that the high diversity of birds suppresses lizard abundance by both a competition for insect prey resources and predation of all life stages of lizards? Lizard abundance may also be suppressed by forest-floor fires (P. P. van Dijk, pers. comm.) that occur moderately frequently in these dry dipterocarp forests.

Another comparison of the amphibian fauna is possible with Ma Da, Vietnam, approximately 650 km south-east of Sakaerat. This site is primarily secondary forest with scattered stands (a hectare or less) of primary dipterocarp forest (Tarkhnishvili, 1994). Nineteen species of frog occur at Ma Da. Eight species are shared with Chatthin and 11 species with Sakaerat. This comparison and the one with Sakaerat are, of course, dependent upon the correct identification of the amphibians and species, as well as the assumption that a named taxon in Myanmar is the same as the one in Thailand as in Vietnam. In spite of these potential difficulties, the Chatthin frog fauna shows decreasing similarities with increasing distance even though the structure of the habitat appears similar.

The Thai and Vietnamese frog faunas suggest that the central Myanmar fauna has closer biogeographic affinities with the south-east Asian one than to the Indian fauna. Chanda's (1994) report on the north-east Indian frog fauna lists 54 species. Chatthin shares only five species with this area that is geographically closer than the south-east Asian sites. This lack of shared fauna reinforces Chanda's conclusion that the frog fauna of north-eastern India is largely derived from the Indian subcontinent.

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The investigation of the Chatthin herpetofauna owes its support and thanks to numerous individuals and organizations. We wish to thank the Myanmar Ministry of Forestry and its Division of Nature and Wildlife Conservation (U Uga, Director) for encouraging the collaborative programs between the wildlife division staff and Smithsonian research scientists. Many members of the Chatthin Wildlife Sanctuary community have caught or drawn our attention to unique specimens of the herpetofauna, and some have joined us in our various surveys; we greatly appreciate their labours and encouragement. British Airways has generously provided transportation for GZ and his field gear. The Smithsonian Biological Survey and Inventory Program has provided funding to permit the year around inventory and monitoring program, as

well as for field equipment and supplies and GZ's in-country expenses. We also note our special appreciation to C. Wemmer for his enthusiastic encouragement of studies of the Burmese biota. P. Zug assisted us with data entry and analysis. We thank A. M. Bauer and P. P. van Dijk for their advice that improved the accuracy and clarity of this report.

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APPENDIX I

Representative voucher specimens of the Chatthin herpetofauna. For brevity, we have not listed all specimens examined but provide one or more voucher records for each

species occurring in Chatthin Wildlife Sanctuary. Abbreviation: ChWS, Chatthin Wildlife Sanctuary collection; USNM, National Museum of Natural History, Smithsonian Institution.

AMPHIBIA

Anura. Family Bufonidae, *Bufo melanostictus*, USNM 520316-17. Family Microhylidae, *Glyphoglossus molossus*, USNM 520318-20; *Kalophrynus interlineatus*, USNM 520321; *Kaloula pulchra*, USNM 520322-31; *Microhyla ornata*, USNM 520349-67; *Microhyla* sp., USNM 520333-48. Family Ranidae, *Occidozyga lima*, USNM 520368-82; *Rana lateralis*, USNM 520399-405; *Rana limncharis*, USNM 520438-50; *Rana limncharis*/small, USNM 520406-20; *Rana macrodactyla*, USNM 520469; *Rana rugulosa*, USNM 520470-80; *Rana tigrina*, ChWS 34195; *Tomopterna breviceps*, USNM 520490-499. Family Rhacophoridae, *Chirixalus nongkhorensis* USNM 520503-20; *Polypedates leucomystax*, USNM 52035-39.

REPTILIA

Testudines. Family Testudinidae, *Indotestudo elongata* USNM 520645. Family Trionychidae, *Lissemys scutata*, USNM 520643-44.

Squamata/lizards. Family Agamidae, *Calotes mystaceus*, USNM 520540-41; *Calotes versicolor*, USNM 520542-47; *Leiolepis peguensis*, USNM 524046. Family Gekkonidae, *Gekko gekko*, USNM 520548; *Hemidactylus bowringii*, USNM 520551-57; *Hemidactylus frenatus*, USNM 520560-65. Family Scincidae, *Lygosoma lineolatum*, USNM 520566-75; *Mabuya dissimilis*, USNM 520631-14; *Mabuya novemcarinata*, ChWS 34127; *Mabuya quadricarinata*, USNM 520616; *Sphenomorphus maculatus*, USNM 520618-21. Family Varanidae, *Varanus bengalensis*, ChWS 34194.

Squamata/snakes. Family Colubridae, *Ahaetulla nasuta*, ChWS 34147; *Amphiesma stolatum*, USNM 520630-34; *Boiga multomaculata*, USNM 520622; *Boiga ochracea*, USNM 524064; *Chrysopelea ornata*, USNM 520623; *Dendrelaphis subocularis*, USNM 524066; *Elaphe radiata*, USNM 524067; *Lycodon aulicus*, USNM 520627-29; *Oligodon cruentatus*, USNM 524068; *Oligodon quadrilineatus*, USNM 52064-25; *Oligodon splendidus*, USNM 520626; *Ptyas mucosus*, ChWS 34174; *Sibynophis collaris*, ChWS 34154. Family Cyliodrophidae, *Cylindrophis rufus*, ChWS unnumbered. Family Elapidae, *Bungarus fasciatus*, USNM 520635-36; *Naja kaouthia*, USNM 524075. Family Typhlopidae, *Ramphotyphlops braminus*, USNM 520637-42. Family Viperidae, *Daboia russelii*, USNM 524077; *Trimeresurus erythurus*, USNM 524076. Family Xenopeltidae, *Xenopeltis unicolor*, USNM 524062.

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STRUCTURE AND FUNCTION OF TRACHEAL AIR SACS IN THE ASIAN SNAKE *GONYOSOMA OXYCEPHALUM*

Harvey B. Lillywhite and Tamir M. Ellis

Department of Zoology, University of Florida, Gainesville, Florida 32611-8525, U.S.A.

Email: hbl@zoo.ufl.edu

(with three text-figures)

ABSTRACT. - The gross structure of tracheal air sacs (diverticula) and their use in defensive displays were examined in the Asian rat snake *Gonyosoma oxycephalum*. Tracheal air sacs are non-respiratory structures that are anatomically distinct from the lung and tracheal airway. They function in *Gonyosoma* to inflate the neck and thereby exaggerate vertical neck displays during defensive postures. In this context tracheal air sacs represent alternative specializations, inasmuch as inflation and display of the neck are achieved in other species by use of a distensible tracheal airway. The evolution of tracheal air sacs has resulted in striking morphological divergence at low taxonomic levels, yet their origin and adaptive significance remain elusive.

KEY WORDS.- Snakes, *Gonyosoma oxycephalum*, air sacs, tracheal diverticula, trachea, lung, neck displays.

INTRODUCTION

Non-pulmonary, saccular extensions of the trachea have been documented in 32 species of Asian snakes (Young, 1992). These structures are thin-walled, membranous compartments and have been termed air sacs, avascular tracheal chambers (Wallach, 1998), atrabecular multicameral tracheal organ (Wallach, 1998), neck sacs (Beddard, 1903), and tracheal diverticula (Young, 1992). While these unusual structures provide one of few documented examples of extrapulmonary air sacs in non-avian vertebrates, they have received little attention from biologists. There are few detailed anatomic descriptions, and very little functional investigation or interpretation of these structures. In recent reviews, Young (1992) and Van Wallach (1998) have examined the variation of diverticula and discussed the possible evolution of these structures.

The Asian colubrid snake *Gonyosoma oxycephalum* possesses well-developed tracheal air sacs which are inflated to produce impressive neck displays that are used in defense (Fig. 1). Here we describe the anatomy of the air sacs in *Gonyosoma*, and we discuss their relationship to defensive neck displays.

MATERIALS AND METHODS

We observed behaviour in four snakes and examined tissues of six freshly killed snakes, all from Thailand. Four specimens were dissected in Bangkok, and five others were obtained from a supplier in Florida. Live snakes were observed and photographed outdoors in situations where we approached freely moving specimens in attempts to evoke defensive behaviour. Fresh tissues were examined in snakes that were killed by an overdose of sodium pentobarbital as part of another study. We intubated the trachea to observe the inflation of air sacs during controlled introduction of pressurized air.

To observe the internal anatomy of air sacs, we exposed tissues by means of a ventrolateral incision along the length of the neck (Fig. 2). The origins, number and configuration of the structures was examined by pulling and probing of soft tissues. The tracheal membrane was exposed by a secondary incision along the trachea. We recorded the mass and length of each snake, the length of trachea, vascular lung and saccular lung, heart position, and the number of air sacs. We found it difficult to determine precisely where the thin and delicate saccular lung terminated posteriorly. Thus, in some specimens it

TABLE 1: Relative lengths of lung segments measured in six specimens of *Gonyosoma oxycephalum*. Data are means \pm SD, with range in parentheses. * The measurement for saccular lung, hence also total lung, could not be determined in two specimens. Thus, means for these parameters are based on four individuals instead of six.

	Tracheal segment	Vascular lung	Saccular lung*	Total lung*
Length, cm	28.6 \pm 3.4 (22 - 31)	11.3 \pm 1.4 (10 - 13)	89.8 \pm 1.9 (88.5 - 92)	132.2 \pm 2.5 (130.5 - 135)
% SV Length	22.3 \pm 0.7 (21.1 - 23.1)	9.0 \pm 1.3 (8 - 11)	63.9 \pm 0.9 (63.1 - 64.8)	94.3 \pm 0.8 (93.6 - 95.1)
% Total Length	15.1 \pm 0.9 (14.3 - 16.8)	6.8 \pm 0.7 (5.9 - 7.6)	50.0 \pm 1.4 (48.9 - 51.5)	73.6 \pm 2.3 (72.1 - 76.3)

was necessary to inject coloured water into the lung to determine its termination within the body cavity. The water was moved posteriad by gravity until it dammed within the blind termination. In one snake, the trachea and associated structures were dissected free, then inflated with flowing air to produce an air-dried preparation for additional observation. Data for anatomical measurements are reported as means \pm SD.

RESULTS

Anatomy. - The snakes studied had a mean mass of 296 ± 92.7 g and averaged 169 ± 18.9 cm in total length. The tail occupied $23.7 \pm 2.8\%$ of the total length.

Like other colubrid species, *Gonyosoma* possesses a total lung structure consisting of three parts: (1) an anterior, nonvascular segment comprised of the trachea; (2) a short vascular segment consisting of respiratory parenchyma (sometimes termed "bronchial lung"); and (3) a very thin, saccular segment extending from the respiratory parenchyma to the posterior region of the body cavity. The mean lengths of the respective segments, and their percentages of body length, are given in Table 1. Anteriorly, the tracheal segment is a simple tube consisting of half-circular, incomplete cartilage rings connected at their opposing tips by a thin, low-compliant, non-respiratory strip of membrane that forms the dorsal tracheal airway. Posteriorly, the saccular segment consists of thin, compliant, non-respiratory membrane.

Three of six specimens possessed dual vascular lungs, the left one being less developed and diminutive compared with the right. The left and right vascular lungs did not differ appreciably in length, however. The anterior aspect of the vascular lung(s) terminated at or very near the heart,

which was located $18.5 \pm 0.7\%$ of the total body length from the head. The posteriormost cartilage of the trachea was also located (terminated) near the heart.

Anatomically distinct air sacs are associated with the trachea for a distance extending between the head and heart (about 16% of total body length). They consist of thin, membranous compartments whose lateral walls extend ventrally from the dorsolateral margins of the tracheal cartilage. Transverse membranes partition the subtracheal space to form 11-15 separate compartments, each adjoining its neighbour by a common septum (Fig. 2; 3 top). Air communicates between the trachea and each individual air sac by means of a single foramen situated at the left dorsal margins of the tracheal cartilage and immediately beneath the "roof" of the air sac (Fig. 3 centre). There is a longitudinal series of circular regions where the tracheal wall is thin or eroded, suggesting early stages of incomplete foramina (Fig. 3 centre). However, only one foramen actually perforates the tracheal airway per individual air sac. Tissues investing the air sacs consist of a thin membranous sheet of connective tissue overlain by muscle (Fig. 3 bottom).

To quantify variation in the sizes of individual air sacs, we measured their lengths, septum to septum, in two different snakes. Air sacs varied from 10 to 19 mm in length and averaged 15.8 ± 5.5 and 17.1 ± 6.0 mm, respectively, in the two individuals.

Mechanics and behaviour. - Air sacs in *Gonyosoma* could be readily inflated with comparatively little expansion of the dorsal tracheal airway, which is far less compliant. Expansion of the air sacs extended the skin of the neck ventrally and somewhat outward, as is seen in defensive displays. Observations of living snakes

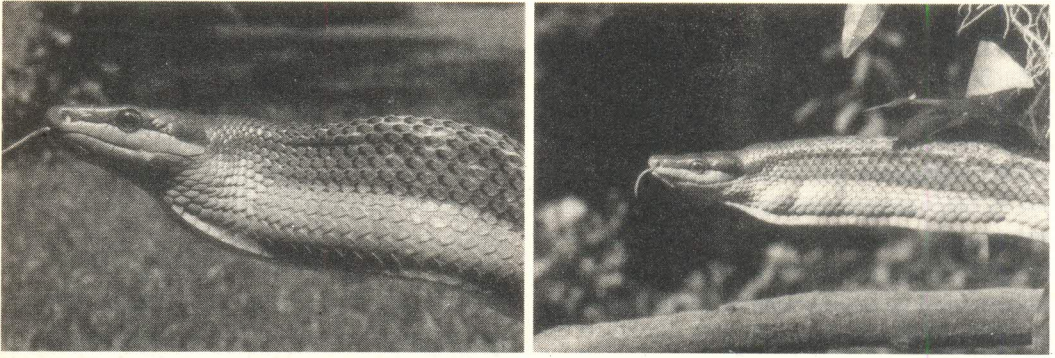


FIGURE 1: Vertical neck displays in *Gonyosoma oxycephalum*. Left: Typical display in which the neck is laterally compressed and the ventral body extended, due in part to inflation of the tracheal air sacs. Right: Lateral view of a disturbed specimen moving through vegetation. Protrusions of the ventral neck are attributable to individual air sacs of which several can be seen in outline just behind the head. This display included much of the body (to right of photograph) in addition to the neck.

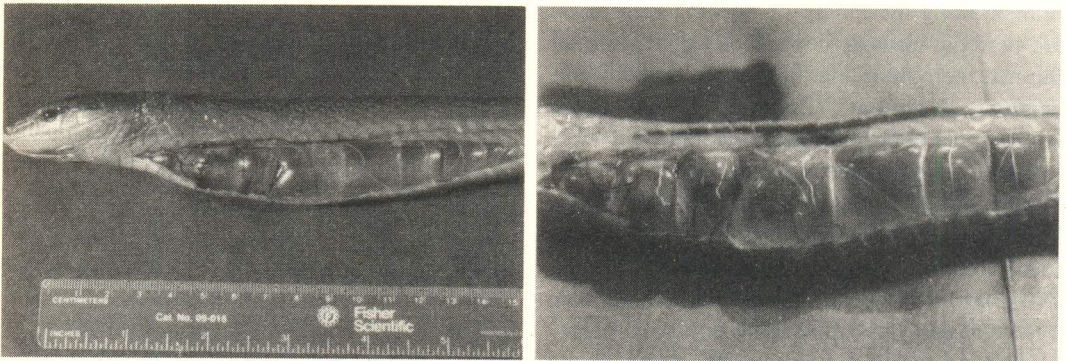


FIGURE 2: Left: Inflated tracheal air sacs exposed in the neck of *Gonyosoma oxycephalum*. Collectively, all of the units appear to comprise one elongate, nonvascular structure with membranous attachment to the dorsal horns of tracheal cartilage, extending between the heart and head. Right: Closer view of above, showing that individual air sacs are formed by thin, transverse septa which subdivide the primary compartment.

indicated that controlled use of body muscles allows various parts of the pulmonary system to be inflated independently.

We provoked defensive behaviour in *Gonyosoma* by approaching or harassing unrestrained snakes outdoors. Snakes produced vertical neck displays in which the gular region was extended ventrally, and the body was laterally compressed. The lateral compression was especially prominent beneath the level of the ribs and in the neck region where the air sacs were present (Fig. 1 left). However, some displays involved lateral compression along half or more of the

body length (Fig. 1 right). The visual effect of air sac inflation was to enlarge the anterior region of display.

DISCUSSION

Morphology and mechanics. - Tracheal air sacs of *Gonyosoma oxycephalum* are derived from the tracheal airway (see also Young, 1991), but are secondary and accessory components of the pulmonary system. They are located in the ventral portion of the body cavity immediately below the trachea, which is located near the dorsal body wall. The air sacs are thin, fragile, translu-

cent, poorly vascularized, and completely removed from the highly vascular pulmonary parenchyma posterior of the heart. These structures do not receive branches of the pulmonary artery, and they cannot have a significant direct role in respiratory gas exchange (Brongersma, 1957). The vascular lung containing the pulmonary vasculature of *Gonyosoma* has a position and gross morphology that appears to be typical of other arboreal and terrestrial colubrid species (Stinner, 1982; Lillywhite, 1987).

The tracheal membrane superior to, and adjoining, the tips of the tracheal rings is periodically perforated with foramina to yield a single perforation per each associated individual air sac (Fig. 3 centre). The size of the foramina exhibits variation, which is reported to range from 1.1 to 7.7 mm (Young, 1991). Located between the foramina along the length of tracheal membrane are periodic circular depressions or regions of thinned membrane that have been termed "imperforate foramina" (Beddard, 1903). These structures have been suggested to represent "normal perforations that have been covered by a thin membrane" (Young, 1991). It is equally likely, however, that these are immature stages of foramen evolution ("incipient diverticula" of Young, 1992; see also Beddard, 1903 and Thompson, 1914). That is, the imperforate formamina represent tissue responses to developmental events and selection forces that have produced the completed foramina. The question remains, Why have either complete foramina been covered by a membrane, or incomplete foramina not developed to form an actual perforation? Young (1992) suggested these structures might represent very small, poorly expanded diverticula, possibly indicating how these structures could have evolved *de novo*. Mystery remains, however, concerning the selection force(s) that produced such structures, regardless of how we interpret them (see below). In snakes having multicameral lungs, foramina also pierce the tracheal membrane and lead to the separate respiratory chambers, typically one foramen per chamber (Wallach, 1998).

While there is variation in the number and size of air sacs along the length of associated tra-

chea, the multiple compartments probably stabilize the distribution of air during inflation of the ventral neck region. It appears the air sacs could be filled with air in two different ways. First, extension of the ventral neck might lower pressure within the saccular air spaces and thereby induce filling by an aspiration mechanism. Second, air might inflate the sacs by means of positive pressures involving compression of the tracheal airway or the adjoining vascular and saccular lung. Observations of snakes producing prominent neck displays reveal bulging outlines of individual air sacs (Fig. 1 right), suggesting these structures are inflated by a positive pressure mechanism (see also Gans and Richmond, 1957). Little attention has been given to the fact that the air sac membrane is overlain by layers of muscle (Fig. 3 bottom) (Young, 1991). Thus, it would be of considerable interest to investigate whether air sac volumes are controlled solely by adjoining lung pressures and movements of the body wall, or, in addition, by the contractile actions of muscle exerting forces directly upon the saccular membranes.

Function.—Young (1991) and Wallach (1998) have discussed five possible functions of the tracheal air sacs of snakes, namely (1) to increase available air, (2) provision of accessory sites for gas exchange, (3) enhancement of buoyancy, (4) neck inflation, and (5) acoustic modification of defensive hissing. For reasons we shall not repeat here, Young concluded that only two functions, sound production and neck inflation, are plausible. Of these possible functions, only sound production has been investigated experimentally. Tracheal air sacs appear to act as resonating chambers and modify the acoustic profile of hissing sounds (Young, 1991). Sound production in the species tested (*Ophiophagus hannah* and *Gonyosoma oxycephalum*) was normally associated with inflation of the neck. Therefore, it is possible that acoustic modification of hissing sounds is an inadvertent result of neck inflation and has no adaptive function by itself. In our observations of *G. oxycephalum*, neck displays were easily evoked when snakes were disturbed, but they seldom engaged in hissing.

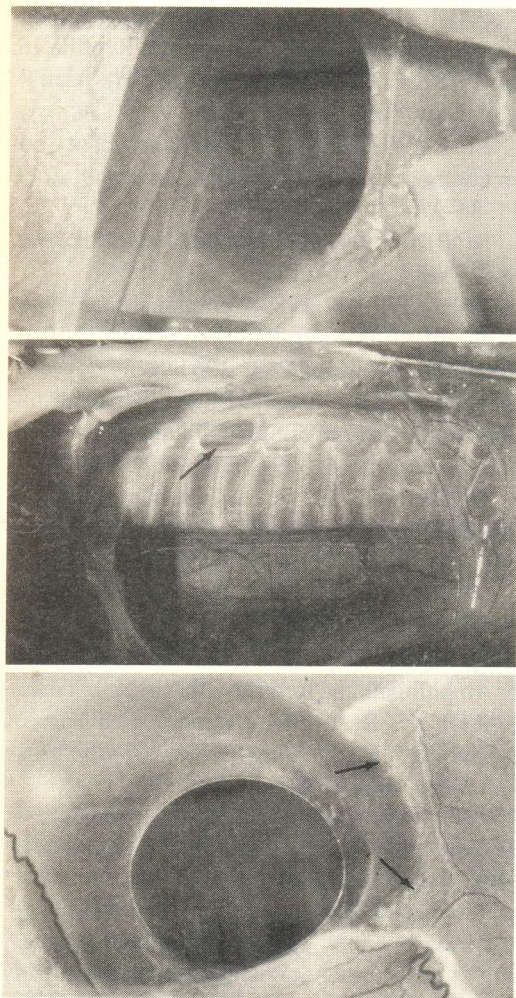


FIGURE 3: Views of a single air sac in *Gonyosoma oxycephalum*. Top: Lateral view looking into an individual air sac, showing the dorsal trachea and the anterior transverse septum (to left of centre) which adjoins the neighboring unit. Centre: Lateral view of the trachea from within an air sac, showing the foramen leading to the tracheal airway at its left side (arrow). Note there is a longitudinal series of circular regions to either side of the foramen where the airway wall is thinned or eroded, suggesting early stages of incomplete (imperforate) foramina. Only one foramen actually perforates the tracheal airway per individual air sac. Bottom: Artificial hole created by a pin prick in the ventral wall of an air sac. The view inside looks dorsally onto the ventral aspect of the trachea. Tissue investing the air sac consists of a thin membranous sheet overlain by muscle (arrows).

The taxonomic distribution of tracheal air sacs is peculiar, involving several families and subfamilies, and species that are restricted to central and southern Asia. Except for *Ophiophagus hannah*, all other species are colubrids, and most are arboreal or have tendencies to climbing. It appears that all of the genera, and probably all of the species, which possess tracheal air sacs also engage in some form of expanded neck display. Thus, it seems compelling to conclude that evolution of these accessory extrapulmonary structures is somehow related to expansion or distension of the neck as antipredatory defensive displays (Greene, 1988). Various neck displays are accomplished in other species of snakes which lack tracheal air sacs, however, and the neck can be inflated by means of a distensible tracheal airway (e.g., Noble, 1921). Thus, the tracheal air sacs of *Gonyosoma* and other extant forms may represent alternative specializations. Air sacs are present in *O. hannah*, but evidently absent in other species of cobra. And, within a single genus, air sacs are present in *Ptyas korros* but not in *P. mucosus*. Clearly, the evolution of air sacs has produced striking morphological divergence at low taxonomic levels.

The selection forces and evolutionary mechanisms that have produced these complex structures seem likely related to neck inflation, whether for enhancement of visual displays or acoustic signalling. Alternatively, it has been suggested that non-respiratory tracheal chambers are a simplification or degeneration of a vascularized structure that was present in ancestral forms (Wallach, 1998). The respiratory "tracheal lung" probably evolved early during the radiation of snakes and was subsequently modified or lost in various phyletic lines (Beddard, 1906; Underwood, 1967; Wallach, 1998). We must acknowledge the possibility that tracheal air sacs might have no function that is presently maintained by natural selection. Thus, further work is required to shed light on the origin(s) of both tracheal lungs and the non-respiratory air sacs that are possibly derived from them.

ACKNOWLEDGEMENTS

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A NEW SPECIES OF *TENUIDACTYLUS* (SAURIA: GEKKONIDAE) FROM BALOCHISTAN, PAKISTAN

Khalid J. Baig

Pakistan Museum of Natural History,
Garden Avenue, Shakerparian, Islamabad 44000, Pakistan
Email: nathist@pmnh.sdnpc.undp.org
(with two text-figures)

ABSTRACT.- A new species of *Tenuidactylus* is described from the Toba Kakar Range of north-eastern Balochistan, Pakistan. *Tenuidactylus rhodocaudus* sp. nov. is montane in distribution, and found between 1,800-2,400 m above msl. It can be differentiated from congeners in showing a low midventral count (16-18); 23 preano-femoral pores in males; five to nine preanal pores in females; and a black and pink banded tail, with two rows of spinose tubercles.

KEY WORDS.- Systematics, Sauria, Gekkonidae, *Tenuidactylus rhodocaudus*, new species, Balochistan, Pakistan.

INTRODUCTION

The taxonomy of Palaearctic bent-toed gekkonids has been reviewed or commented on by Smith (1935), Underwood (1954), Minton (1966), Mertens (1969), Szczerbak and Golubev (1984), Böhme (1985), and Bauer (1987), and those from the former USSR and adjacent countries were subject to a detailed review by Szczerbak and Golubev (1986). The last mentioned work divided the genus *Tenuidactylus* into three subgenera- *Tenuidactylus*, *Cyrtopodion* and *Mediodactylus*. Khan (1989; 1991) discussed the taxonomy of *Tenuidactylus* species from Pakistan, attempting to revise the systematic arrangement of species found in Pakistan on the basis of morphological characters and elevated the subgeneric status of these gekkonids to that of full genera.

Five of seven species of *Tenuidactylus* species from Pakistan were described within this decade (Khan, 1989; 1991; 1993a; Khan and Baig, 1992; Khan and Tasnim, 1990). Surprisingly, Khan (1993c) did not report *Tenuidactylus* from Balochistan, which comprises a third of the territory of Pakistan, although *T. kohsulaimanai* Khan, 1991 and *T. fortmunroi* Khan, 1993b, have been described from areas adjacent to Balochistan. Leviton and Anderson (1970) reported 18 species of gekkonids from Afghani-

stan, of which *fedtschenkoi* and *caspius* belong to *Tenuidactylus*. Clark (1990) reported the presence of *caspius*, *longipes* and *turcmenicus* from Afghanistan, and mentioned that the records of *fedtschenkoi* were based on misidentifications. Both Anderson (1974) and Clark (1991) indicated the presence of *caspius* and *fedtschenkoi* from eastern Iran bordering Pakistan's Balochistan Province. However, none of these have been reported from within the boundaries of Pakistan so far (fide Smith, 1935; Minton, 1966; Mertens, 1969; Khan, 1993c).

A new species of *Tenuidactylus* is described here from Pakistan's Balochistan Province. The type series have been deposited at the Pakistan Museum of Natural History (PMNH).

Tenuidactylus rhodocaudus sp. nov.

(Fig. 1)

Holotype.- PMNH 749, an adult male, from Tanishpa (31° 12'N; 68° 28'E), District Kila Saifullah, Balochistan, Toba Kakar Range, Pakistan, elevation 2,320 m. Collected by K. J. Baig, 25 May, 1997.

Paratypes.- PMNH 747-748, 750-756, 758-760 (12 paratypes), same data as holotype. Sex indicated in Table 1; PMNH 757, from the sandy desert at Ashewat (31° 25'N; 68° 30'E),

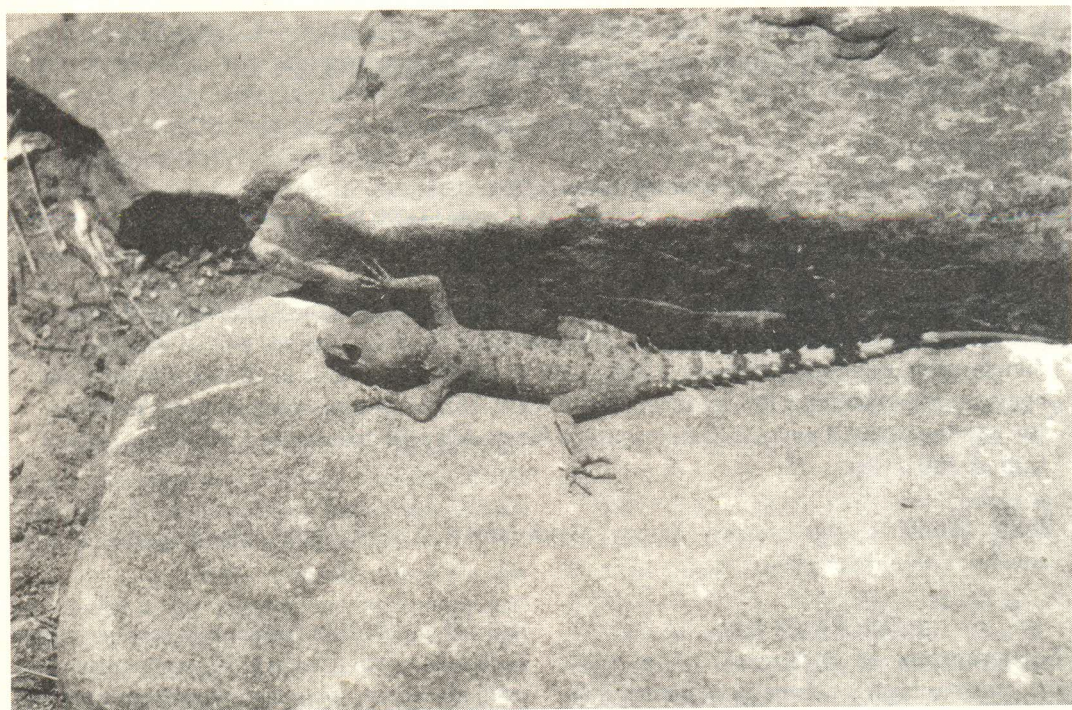


FIGURE 1: Dorsolateral view of the holotype of *Tenuidactylus rhodocaudus* sp. nov. (PMNH 749) in life.

elevation 1,840 m. Collected by K. J. Baig, 26 May, 1997. The type localities are shown in Fig. 2.

Diagnosis.- Habitus robust; 12-14 longitudinal rows of smooth or feebly keeled, enlarged tubercles; nostril surrounded by rostral, supralabial I and three nasals; upper nasals separated by a single internasal; 16-18 scales across midbelly; 92-106 midventral scales between mental and vent; males with continuous series of 23 preano-femoral pores; lateral digital fringes absent; females with five to nine preanal pores; tail segmented, with two rows of spinose tubercles on the lateral aspects and is banded with pink and black in life.

Description of holotype.- Habitus robust; body elongated, moderately depressed; rostral rectangular, incompletely divided by a median furrow; nostrils small, oval or rounded, bordered by rostral, supralabial I and three nasals; upper nasals separated by a single internasal; forehead with tuberculate, juxtaposed scales; scales on supraorbital region flat and largest of the head scales; enlarged tuberculated scales scattered on

head; 13 scales between posterior corner of eyes and ear opening; 12/13 scales in a row adjacent to supralabials between nasal and preocular; a parabolic fold between eye and ear opening; four rows of supraciliaries; 18 scales in outermost row; four large supraoculars; five small interorbitals; 10 supralabials; 8/9 infralabials; anterior infralabials relatively large; mental triangular, large; three postmentals, the first in contact with each other; gular scales large, juxtaposed; scales on neck and chest imbricate; 16 scales at midbelly; 87 midventrals; underside of thigh and shank with large scales; no gular fold; 23 preanofemoral pores.

Body dorsum with 12 longitudinal rows of enlarged, smooth or weakly keeled tubercles, each surrounded by nine and separated by 1-5 juxtaposed, granular scales. Limbs moderately long, not very strong, when adpressed reaching the level of the neck, covered with small, smooth scales intermixed with enlarged keeled scales.

Tail longer than head and body; depressed; swollen at base, with two postanal apertures bor-

TABLE 1: Measurements and scale counts of the type series of *Tenuidactylus rhodocaudus* sp. nov. Measurements in mm. Abbreviations: m = male; f = female; j = juvenile; SVL = snout-vent length; TL = tail length; HL = head length; HW = head width; SN = snout length; E-E = eye to ear distance; IN = internasals; SL = supralabials; IL = infralabials; PM = postmentals; DT = number of dorsal tubercles; SB = scales across belly; PP = preanal pores; FP = femoral pores; T4 = lamellae under toe IV; LT = laticaudal tubercles; MV = midventrals.

	PMNH 747	PMNH 748	PMNH 749	PMNH 750	PMNH 751	PMNH 752	PMNH 753	PMNH 754	PMNH 755	PMNH 756	PMNH 757	PMNH 758	PMNH 759	PMNH 760
Sex	f	m	m	m	f	m	f	m	f	f	f	j	j	j
SVL	64.0	59.0	59.0	59.3	61.0	61.5	60.4	45.0	50.0	56.0	47.5	35.0	28.0	30.0
TL	br	reg	74.0	-	br	br	br	reg	br	br	57.0	45.0	33.0	31.0
HL	17.0	17.0	16.3	16.6	17.0	17.0	16.3	13.3	14.2	14.8	13.5	11.0	8.3	9.8
HW	12.0	12.3	12.0	12.0	12.3	12.2	12.3	9.4	9.4	9.8	9.4	7.8	6.0	6.5
SN	7.4	6.5	7.0	6.9	7.3	7.0	6.5	5.5	5.5	6.0	5.0	3.5	2.3	3.2
E-E	5.4	5.3	5.0	4.8	5.1	5.0	4.8	3.2	3.5	3.7	3.5	2.3	1.8	2.2
IN	1	1	1	1	1	1	1	1	1	1	1	1	1	1
SL	9	10	10	10	10	9	9	9	10	9	8	10	9	9
IL	7	7	8	8	8	7	7	8	9	7	8	9	8	9
PM	3	3	3	3	3	3	3	3	3	3	3	3	3	3
DT	14	14	12	14	14	14	14	14	14	14	14	12	14	12
SB	17	16	16	17	18	16	18	18	18	18	18	18	14	16
PP	5	9	9	9	7	9	5	9	5	5	9	-	-	-
FP	absent	7+7	7+7	7+7	absent	7+7	absent	7+7	absent	absent	absent	-	-	-
T4	22	24	23	23	23	22	23	23	24	24	23	25	24	23
LT	2	2	2	2	2	2	2	2	2	2	2	2	2	2
MV	100	100	94	96	102	106	96	90	95	106	92	98	94	97

dered by intramembranous ossification, verticellate, segmented. Each segment consists of 5-6 rows of small scales dorsally and two large scales arranged in a single row ventrally. Tail base with small scales arranged in five rows, each consisting of 5-6 scales; two dorsolateral rows of enlarged spinose tubercles laterally; these gradually becoming smaller towards distal end and become indistinct near tip.

Digits long, thin; distal part bent; scansors under finger III 17; under toe IV 23; those on joints of digits distinctly enlarged; claws sharp, short, arising between a pair of scales, of which distal is largest and notched; no lateral digital fringes; a single row of smooth subdigital lamellae under each digit.

Dorsum of body in life with dark brown speckling, arranged in nine indistinct broken cross-bands, on a dusty ground colour. Dorsal scales contain tiny pigmented granules. The granules extend over some ventral scales which lie adjacent to dorsals. Ventral scales white or

cream. Tail with alternating bands of pink and black, both dorsally and ventrally, most distinct in midtail region, where bands are broader and in greater contrast.

Etymology.- Latin for rosy-tailed, in allusion to the pink bands on the tail. Noun in apposition.

Measurements of holotype (in mm).- Snout-vent length (SVL) 59.0; tail length 74.0; head length 16.0; head width 11.5; head depth 5.5; eye diameter 3.8; ear opening 1.7/1.0; forelimb length 24.5; hindlimb length 35.0.

Variation and sexual dimorphism.- Variation in morphological features, including size and pholidosis has been summarized in Table 1. Sexual dimorphism is marked. A continuous series of preano-femoral pores characterise adult males, while adult females possess only preanal pores. In juveniles of both sexes, these pores are not visible, although feeble pits are seen. A pair of postanal pores are present at tail base in both sexes, being marked and bordered with cloacal bone in males.

Transverse bands on the body are sometimes distinct (e.g., PMNH 751, 754, 756) or indistinct (e.g., PMNH 749, 752, 753). Tail bands are also variable, being relatively most distinct in juveniles.

Natural history.- The new species was found in crevices and undersurfaces of sandstone slabs near watercourses. I found the species to be typically crepuscular, although it could also be seen during the day.

The presence of eggs in some females, and of juveniles in the type series that were obtained in May indicate that April-July is the reproductive season. Eggshells were seen glued on the hill slopes and on the undersurfaces of sandstone. The presence of several eggshells at a single site suggests that egg-laying sites are communal in this species. The sex ratio, from data in Table 1, appears to be not different from 1:1.

Tanishpa, one of the type localities of the new species, is a small town, situated at an altitude of

2,400 m above msl in the Toba Kakar Range. The area is a Game Reserve established for the conservation of the urial (*Ovis orientalis*) and markhor (*Capra falconeri jerdoni*). The region can be characterised as dry temperate, with sparse vegetation. In the spring, seasonal flowers, including that of *Eremurus stenophylus*, are seen in the valley. Wild pistachio (*Pistacia khinjuk*), locally referred to as ‘Ushgai’, is relatively common, and in places where water is available, orchids are cultivated. In general, the area receives very little rainfall, and winters are severe.

COMPARISONS

Within the genus *Tenuidactylus*, two groups are identifiable, one with large trihedral/strongly keeled dorsal tubercles (e.g., *montiumsalsorum* and *kohsulaimanai*), the other with moderately enlarged, smooth or weakly keeled dorsal tubercles (e.g., *rohtasfortai* and *indusoani*). Table 2 summarises characters that can be used to differ-

TABLE 2: Comparison of morphological features of Palaearctic bent-toed gekkonids from Pakistan and neighbouring countries. Measurements in mm. + = present; - = absent; NA = data not available; fb kl = feebly keeled; dep = depressed; fb dep = feebly depressed; md = rounded; trihed = trihedral; fm = femoral; SVL= snout-vent length; RTL = relative tail length; SL = supralabials; IL = infralabials; PM = postmentals; DS = dorsal tubercle shape; DT = number of dorsal tubercles; MV = midventrals; SB = scales across belly; PP = preanal pores; FP = femoral pores; PFP = preanofemoral pores; T4 = lamellae under toe IV; LT = laticaudal tubercles; TS = tail shape.

Species names	SVL (max)	RTL	SL	IL	PM	DS	DT	MV	SB	PP	FP	PFP	T4	LT	TS
<i>stoliczkai</i>	55.0	< SVL	9-11	8-9	2/3	fb. kl.	scattered	120-149	30-35	-	-	-	NA	3/4	dep
<i>battalensis</i>	73.0	= SVL	9-11	8	2	fb. kl.	12-14	199-205	50-52	8-10	-	-	18-21	2	md
<i>baturensis</i> (females)	53.0	> SVL	9-11	7-9	3	fb. kl.	11	148-150	26-30	-	-	-	24-27	2	dep
<i>indusoani</i>	54.0	> SVL	10-12	8-10	3	fb. kl.	10-12	129-132	21-24	4/5	-	-	27-29	NA	dep
<i>fortmunroi</i>	51.0	> SVL	9-13	8-10	3	flat	12	122-130	22-28	5-8	-	-	22-28	2	dep
<i>scaber</i>	50.0	> SVL	12-13	10-12	NA	trihed.	10-12	NA	20	4-7	-	-	NA	NA	dep
<i>walli</i>	55.0	> SVL	9-10	8-10	2/3	fb.kl.	12-13	160-174	38-40	4	-	-	23-25	3	dep
<i>kohsulaimanai</i>	58.0	> SVL	11	7	3	trihed.	13-14	127-130	27-28	8-10	11-15	35	23-25	3	dep
<i>fedtschenkoi</i>	50.0	> SVL	12-13	11-12	2	trihed.	12-14	NA	27-41	+	+	28-36	NA	NA	fb.dep.
<i>caspius</i>	75.0	> SVL	9-14	7-9	NA	trihed.	12-14	NA	25	+	+	23-31	NA	NA	dep
<i>montiumsalsorum</i>	48.0	> SVL	9-11	8-10	3	trihed.	12-13	NA	21-23	5-7	9-14	26-32	21-23	3	dep
<i>rohtasfortai</i>	55.0	> SVL	9-12	8-10	3	fb.kl.	12	102-135	24-31	5-7	6-10	18-27	24	3	dep
<i>rhodocaudus</i>	64.0	> SVL	9-10	7-8	3	fb.kl.	12-14	92-106	16-18	5-9	7-8	23	22-24	2	dep

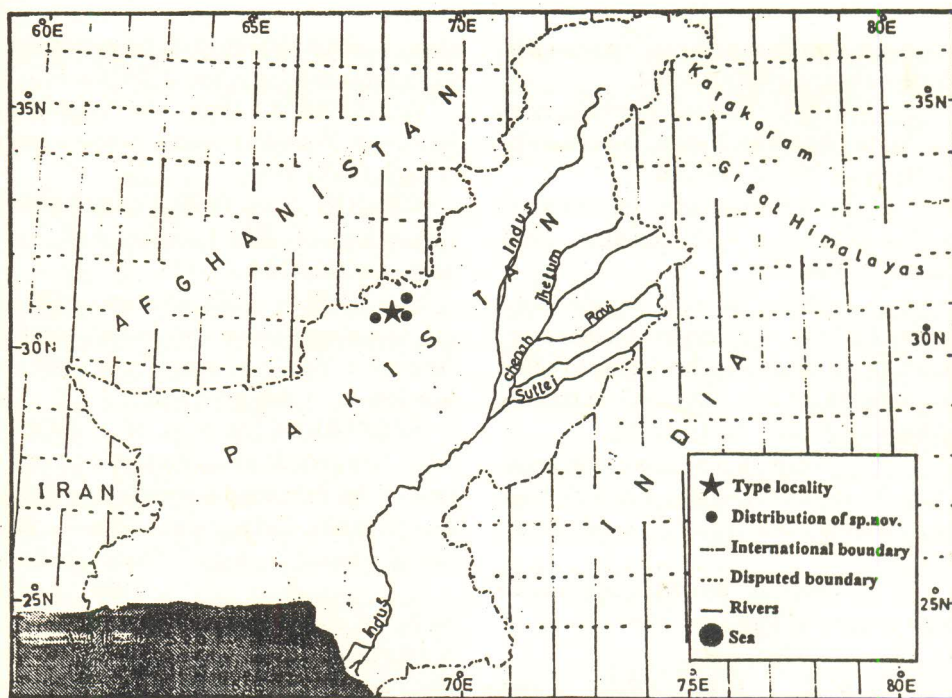


FIGURE 2: Map showing the distribution of *Tenuidactylus rhodocaudus* sp. nov.

entiate these gekkonids from Pakistan and adjacent regions. It is apparent that *Tenuidactylus rohtasfortai* Khan and Tasnim, is the closest congener of *T. rhodocaudus*. However, they differ in the following characteristics: the new species is larger (SVL to 64.0 mm), while *rohtasfortai* does not exceed 55.0 mm. In the latter, infralabials range between 8-10, but never exceeds eight in the new species. Midventrals are typically under 100 in the new species, while being over 100 in *rohtasfortai*. The tail of the new species is distinct in having pink bands and a double row of spinose tubercles on its lateral edge; in *rohtasfortai*, there are three rows of such tubercles. Additionally, the number of scales at midbelly in the new species is the lowest (16-18) reported among all its relatives (Table 2).

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SOUTH ASIAN HERPETOLOGICAL SPECIMENS OF HISTORICAL NOTE IN THE ZOOLOGICAL MUSEUM, BERLIN

Aaron M. Bauer

Department of Biology, Villanova University,
800 Lancaster Avenue, Villanova, Pennsylvania 19085-1699, U.S.A.
Email: abauer@king-kong.csc.vill.edu

ABSTRACT. - The history and growth of the south Asian herpetological collection of the Zoological Museum, Berlin (ZMB) up to 1857 are reviewed, and the status of historically important specimens, including types, is evaluated. The most important ZMB specimens derive from the Bloch collection (amassed in the late 1700's), which served as the source for many of the new species described by Schneider in 1799 and 1801. Most of these specimens probably originated from Tranquebar (Tarangambadi), Tamil Nadu. Additional specimens from India and Sri Lanka, including type material collected by Nietner, Schmarda, Hoffmeister (all from Sri Lanka), and Peters (from Goa) were described by Lichtenstein and von Martens and by Peters. The majority of the 18th and early 19th century types are still extant in the ZMB collection.

KEY WORDS. - Zoological Museum Berlin, type specimens, India, Sri Lanka, history.

INTRODUCTION

The herpetological collection of the Zoological Museum, Berlin (ZMB, a part of the Humboldt-Universität zu Berlin) is among the largest in the world. The collection is perhaps best known for its rich type holdings, derived largely from the work of the former curator and director Wilhelm Peters (1815–1883) (Bauer et al., 1995). The collection, however, extends back in time much earlier than Peters' directorship, which began in 1857. The museum itself was founded in 1810, but received at its inception several older private collections. The most important of these was that compiled by Marcus Eliesar Bloch consisting chiefly of fishes, amphibians, and reptiles. With the Bloch collection as its nucleus, the herpetological collection grew from 405 specimens representing 186 species in 1813 (Peters, 1860a) to 3,604 specimens in 1856, the last full year of the curatorship of Martin Hinrich Carl Lichtenstein. Within the first few years of Peters' directorship a great many more specimens were catalogued so that in 1860 the total stood at 1,005 species represented by 4,911 specimens or specimen lots. Most of the specimens received by the museum during this period of its history were donations or purchases of pri-

vate natural history collections or of material collected by naturalists on expeditions. Because Germany at this time was not united and did not yet possess a colonial empire, the early collections of exotic species were not strongly biased towards any particular part of the world, and material from Africa, South America, and Asia arrived in quantity, despite the absence of a strong formal Prussian presence in many of the countries of origin.

Among the areas strongly represented by this historical material in the Zoological Museum is south Asia. In particular, Tamil Nadu, Bengal, and Sri Lanka are well represented by early Berlin specimens. Some of this material is well-known because it served as type material. For example, specimens in the Bloch collection were described by Schneider (1799, 1801) and Wiegmann (1831), and material collected by Nietner, Schmarda, and others was examined and reported on by Lichtenstein and von Martens (1856) and Peters (1860b, 1861a, 1863b, 1863c, 1871, 1873). Peters even described several new species from among the few herpetological specimens he himself collected at Goa on his return trip from Mozambique in 1847 (Peters, 1854, 1869). Much of the ZMB south Asian material,

however, represented known forms and has never been discussed in the literature, despite its historical importance. In this paper, I present an overview of the south Asian herpetological specimens in the Zoological Museum, Berlin, including types, that were accessioned into the collection, or at least received by the museum, up until the death of Hinrich Lichtenstein (1780–1857), Peters' immediate predecessor as director of the Museum.

MATERIALS AND METHODS

Specimens, catalogues, and archival materials were examined during a series of visits to the Zoological Museum, Berlin during the period 1987–1994. Sources of data consulted include: the modern specimen register (begun in 1856–57), the specimen jar labels (which frequently include the original specimen data as well as any subsequent reidentifications), the card catalogue of ZMB herpetological types (prepared during the middle of the 20th century), and a variety of archival materials providing information regarding the receipt of specimens and collection holdings prior to Peters' assumption of the directorship of the Museum. These archival sources include the *Katalog Inventarium der Amphibien ca. 1822/23*, *Amphibia Musei Regii Berolinensis (1824, 1830)*, *ZMB Eingangs Journal 1811–1857*, and the *Eingangsverzeichnis Amphibien, Fischen, Mollusken, Annulaten, Zoophyten (1842–1850)*. These sources, as well as published papers describing ZMB material from India and Sri Lanka, were used as a guide to compile a list of the material expected to occur in the herpetological collections. Concomitantly, all jars in the herpetological collection were examined to identify any material that had entered the collections in or prior to 1857.

The identification of older material in the Berlin collection was facilitated by the fact that the modern ZMB register of specimens was begun in the last year of Lichtenstein's life in association with the preparation of the published list of the Berlin herpetological holdings in the *Nomenclator Reptilium et Amphibiorum* (Lichtenstein and von Martens, 1856; see below). Any prior numbering schemes were aban-

doned at that time and the existing collections were catalogued sequentially by taxonomic grouping, following the order used in the *Nomenclator*. The ZMB numbers associated with each group of organisms is as follows: ZMB 1–238 (turtles), 239–287 (crocodilians), 288–316 (chamaeleonids), 317–450 (gekkonids), 451–482 (varanids), 483 (helodermatid), 484–676 (iguanids *sensu lato*), 677–825 (agamids), 826–900 (teiids and "microteiids"), 901–1128 (lacertids), 1129–1148 (gerrhosaurids), 1149–1175 (anguids); 1176–1363 (scincids), 1364–5 (pygopodids), 1366–1402 (amphisbaenids), 1403–1434 (scolecophidians), 1435–1458 (uropeltids *sensu lato*), 1459–1537 (boids *sensu lato*), 1538–1542 (acrochordids), 1543–2700 (colubrids), 2701–2821 (terrestrial elapids), 2822–2840 (marine elapids: hydrophiids and laticaudids), 2841–2995 (viperids), 2996–3039 (miscellaneous reptiles), 3040–3088 (ranids and rhacophorids), 3089–3186 (hylids), 3187–3191 (pseudids), 3192–3305 (ranids), 3306–3402 (leptodactylids), 3403–3535 (bufonids), 3536–3563 (microhylids and miscellaneous frogs), 3564–3585 (salamandrids), 3586–3618 (plethodontids), 3619–3620 (hynobiids), 3621–3634 (ambystomatids), 3635–3684 (salamandrids), 3685–3692 (proteids), 3693–3695 (sirenids), 3696 (amphiumid), 3697–3699 (cryptobranchids), 3700–3706 (caecilians), 3706–3750 (miscellaneous amphibians and reptiles). Lichtenstein and von Martens (1856) listed a total of 3,604 specimens present in July 1856. Register entries beginning with 3751 and continuing through 10485 are in Peters' own hand, ceasing on 1 April 1883, just three weeks before his death. The 147 specimens catalogues subsequent to the publication of the *Nomenclator* but prior to Peters' entries appear to represent material processed during the brief period between July 1856 and either Peters' appointment as assistant director of the Museum in December 1856, or Lichtenstein's death in September 1857.

In 1955, 1967, and 1983, under the curatorships of Heinz Wermuth and Günther Peters, partial inventories of the collection were

made in order to determine which of the early specimens were still present. Although many specimens had been lost, my review of the collection indicates that the majority of the first 3,751 herpetological specimens are still present in Berlin and suggests that additional specimens may yet be found. Most ZMB specimens are not individually tagged and the movement of specimens between the labeled jars or the loss of the original jar label can result in the apparent loss of the specimen. Unless they are types that have been figured or have had their measurements recorded, such specimens are extremely difficult to trace.

Specimens which were obviously misidentified were redetermined during my visits to Berlin, but for some problematic groups, identifications are only tentative. In determining the identity of specimens I have relied heavily on the annotations to the ZMB register and jar labels by Wilhelm Peters and many subsequent reviewers and revisors of particular taxonomic groups. Current names of taxa are based on Dutta and Manamendra-Arachchi (1995) and Dutta (1997) for amphibians, and Das (1994, 1997) for reptiles, although subsequent changes have also been incorporated.

THE BLOCH COLLECTION

Marcus (Markus) Elieser (Elisar) Bloch (1723–1799) was a Jewish physician who received his training at the University of Frankfurt an der Oder, then the only university open to Jews in Prussia (Karrer, 1978). Although he was successful in his medical career, Bloch was best known as an ichthyologist and collector of natural history specimens. From the late 1760's onwards, Bloch's collection was noted as one of the finest in Prussia (Karrer, 1978), and he held a prominent position among the growing number of naturalists that lived and worked in Berlin. In 1773, he was among the founders of the Gesellschaft für Naturforschender Freunde zu Berlin (Becker, 1973), an organization that is still extant and which has counted among its members virtually all great German biologists of the last two centuries.

Bloch's natural history contributions fall into two categories: those he made as an author and those he made as a collector. As an author, Bloch's chief contributions were in the field of ichthyology. Approximately 200 names were first proposed in his works on fishes of Germany and the world (Paepke, 1993), which include *Allgemeine Naturgeschichte der Fische* (1782–1795), *Oeconomische Naturgeschichte der Fische Deutschlands* (1782–1784), and *Naturgeschichte der Ausländischen Fische* (1785–1795). In 1801, a posthumous work, *Systema Ichthyologiae* (Bloch and Schneider, 1801), appeared. Bloch's herpetological output was minor, consisting of a series of short papers regarding the North American box turtle (Bloch, 1787, 1788; Bloch in Wallbaum, 1787), that did not propose any new names, and one describing *Lacerta serpens* (a junior synonym of *Lygosoma quadrupes* L.) (Bloch, 1776), with ZMB 1276 (now lost) as its type.

Bloch's natural history collections were extensive and were especially strong in ichthyology, although he also maintained a large herpetological collection as well as holdings of birds, their eggs, and nests. Lichtenstein (1816) indicated the Bloch's fish collection included 1,700 specimens, 1,100 in spirits and 600 dry. Although the exact size of his herpetological collection is unknown, it was clearly substantial by the standards of the day and I have been able to trace at least 380 specimens. On 24 May 1802, several years following Bloch's death, his collections and catalogue were sold to the Königlich Preußische Akademie der Wissenschaften zu Berlin for 4,500 Reichstaler (Karrer, 1978; Karrer et al., 1994). In 1810, these collections (or the bulk of them, as some material appears to have deteriorated in the interim) was turned over to the newly founded Zoological Museum of the University of Berlin.

Bloch's material was generally purchased or otherwise obtained from field collectors and correspondents throughout the world. Perhaps the single largest part of Bloch's herpetological collection was derived from "India orientali" or "Ost-Indien." Much of this material, in turn, seems to have been sent to Bloch by Christoph

Samuel John (1747–1813), a Danish missionary and fellow member of the Gesellschaft für Naturforschender Freunde zu Berlin (Karrer, 1978). John was based in Tranquebar, the modern Tarangambadi (11° 02'N, 79° 51'E), on the Coromandel Coast of Tamil Nadu. This was the site of the Danish East India Company's first headquarters (founded in 1620), and the location of the first Protestant mission in India, founded by the Danes in 1706. With the growth of significance of the other Danish center in India at Serampore (Srirampur), Tranquebar had lost much of its significance by the end of the 18th century; and was finally acquired by the British East India Company in 1845. Although some of Bloch's "East Indian" material originated elsewhere, probably mostly the Indo-Malayan Archipelago, it is clear that many of his specimens were derived from coastal Tamil Nadu. Indeed the missionary John provided Bloch with the Tamil names of both fishes and snakes (Schneider in Bloch and Schneider, 1801 as translated in Karrer et al., 1994; Schneider, 1801).

Although Bloch published nothing on his own south Asian herpetological collections, the material was studied intensively by Johann Gottlob Schneider (1750–1822), Bloch's co-author on the monumental *Systema Ichthyologiae*. Schneider himself was based at the University of Frankfurt an der Oder, first from 1776 as Professor of Philology, and later, after the University's move to Breslau (now Wrocław, Poland) in 1811, as Librarian (from 1814) (Adler 1989). From 1780 onwards, he spent as many as three months per year working with Bloch in Berlin (Karrer et al., 1994), and in the 1790's, he averaged 1–2 months a year as Bloch's house guest, chiefly involved in the study of his amphibian and reptile collection (Karrer, 1978). The material in Bloch's collection was described by Schneider in his *Historia Amphibiorum*, published in two parts in 1799 and 1801. These works contained many descriptions of new taxa, based primarily on the private collections of naturalists and aristocrats throughout Germany. Although many collections were consulted, the collections of Bloch and of the

Hanoverian Lampe were central to Schneider's study.

Schneider completed his major herpetological work prior to the establishment of most of the major modern German institutional museums except the University of Göttingen, which had been founded in 1773 (Böhme and Bischoff, 1984). Unfortunately, many of Schneider's types based on material in private collections, such as that belonging to Linck from Leipzig, have been lost or destroyed over the last two centuries. However, Bloch's material, as noted above, was preserved intact following his death, and in 1810 passed to the Zoological Museum of the University of Berlin. Many of his specimens, including several of Schneider's types, are extant and in excellent condition in Berlin today. Although Bloch's herpetological catalogue has not been located, early records from the Museum, particularly the *Katalog Inventarium der Amphibien ca. 1822/23* provide a clue as to the breadth and depth of the Bloch collection. Based on this information, at least 380 specimens from Bloch must have originally been present in the Museum's collections.

Schneider's (1799, 1801) *Historia Amphibiorum* typically mentioned the museum specimens and literature sources upon which new descriptions were based. Fifteen descriptions of Indian species (or species believed by Schneider to be Indian – see *Bufo guttatus*) appear to be based, in whole or in part, on the Bloch Museum material studied by Schneider in the 1780's and 1790's. Peters (1863a, 1864, 1873) reviewed some of this material and attempted to verify the identity of Schneider's types. One additional Bloch specimen was the basis for a description by Wiegmann (1831), and this too was reviewed by Peters (1860b). The majority of the specimens identified by Peters as types, as well as some others, were located in the ZMB collections during my study. The names based on material from the Bloch collection and their associated type specimens are listed below. The accounts are listed by page order in Schneider (1799, 1801), followed by one account of a Schneider type based on a Lampe specimen in the Berlin collection, and by the Wiegmann

(1831) type. An asterisk (*) is used to denote a specimen confirmed to be present during the period 1987–1994. Current names, if different from the original, are provided.

***Rana cyanophlyctis* Schneider, 1799, *Hist. Amphib. I*: 137.**

Syntypes: ZMB 3197–98*, “ex India orientali,” two specimens sent by John, probably from Tranquebar.

Current Name: *Euphlyctis cyanophlyctis* (Schneider, 1799).

Remarks: These specimens were discussed by Peters (1863a). Frost (1985) indicated that the types had not been traced.

***Rana breviceps* Schneider, 1799, *Hist. Amphib. I*: 140.**

Syntypes: ZMB 3351*(2 specimens), “ex orientali India,” sent by John to Bloch in 1794, probably from Tranquebar (Dubois, 1983).

Current Name: *Tomopterna breviceps* (Schneider, 1799).

Remarks: Bauer et al. (1996) suggested that Schneider had originally proposed this name as a replacement for *Rana gibbosa* L., 1758. However, regardless of Schneider’s intention, he applied a new name to a previously unrecognized taxon, based in part on material from the Bloch collection. Of the five original specimens in Bloch’s collection, Peters (1863a) identified two (catalogued as ZMB 3351). A third specimen, ZMB 3553, was identified as a Bloch specimen more recently (Bauer et al., 1996), but additional evidence from ZMB records indicates that this specimen was obtained as an exchange from the Leiden Museum through Schlegel (possibly in 1849).

***Rana systoma* Schneider, 1799, *Hist. Amphib. I*: 144.**

Syntypes: ZMB 3551*(2 specimens), “ex India orientali.”

Current Name: *Uperodon systoma* (Schneider, 1799).

Remarks: Peters (1863) mentioned only a single specimen under this number, although the description indicates that two specimens were examined by Schneider in the Bloch collection. Frost (1985) indicated that the types had not been traced.

***Bufo melanostictus* Schneider, 1799, *Hist. Amphib. I*: 216.**

Syntypes: ZMB 3462–63*, “ex India orientali.”

Remarks: These specimens were first identified as the types by Peters (1863a). Frost (1985) indicated that the types had not been traced. ZMB 3465, with the same locality and collector, is also present in the collection, but has not previously been regarded as part of the original type series.

***Bufo guttatus* Schneider, 1799, *Hist. Amphib. I*: 218.**

Holotype: ZMB 3517*, “ex India orientali.”

Remarks: Peters (1863a) confirmed that this specimen was Schneider’s type. The locality is in error, as the species, which is valid, is South American. Rivero (1961) corrected the type locality to Surinam. This action appears reasonable given that all of Bloch’s South American material is derived from “Südamerica” or “Surinam.”

***Bufo scaber* Schneider, 1799, *Hist. Amphib. I*: 222.**

Syntype: ZMB 3464*, “ex orientali India.”

Current Name: *Bufo melanostictus* Schneider, 1799

Remarks: Schneider indicated that John had sent several examples of this species, although Peters (1863a) recorded only this specimen as a type.

***Hydrus fasciatus* Schneider, 1799, *Hist. Amphib. I*: 240.**

Syntypes: ZMB 2836, 2837*, no locality stated in description, but listed as “Südamerika” in the ZMB records.

Current Name: *Hydrophis fasciatus* (Schneider, 1799).

Remarks: There were originally four specimens in the Bloch collection, but only these two were identified by Peters (1873). One of these, ZMB 2836, was not located in the Berlin collection in 1993. As noted by Peters (1873), the locality “Südamerika” is obviously incorrect. Smith (1926) referred only to ZMB 2836 as a type and indicated that it was from the “East Indies.” This probably reflects Peters’ earlier correction to the ZMB register. Smith (1926) also

indicated that the type(s) of *Hydrus fasciatus* were collected in 1760. There is no indication as to where this information was derived. It is possible and perhaps probable that these specimens derived from the Bay of Bengal, given Bloch's established connections at Tranquebar, although if Smith's date of collection is correct, the specimens would have been obtained long before John began sending Bloch specimens. Both specimens identified by Peters were listed by McCarthy (1993) as types.

***Crocodilus porosus* Schneider, 1801, *Hist. Amphib. II*: 159.**

Lectotype: ZMB 278*, "Indien."

Remarks: Schneider described the species on the basis of four specimens, three in the Göttingen Museum and one in the Bloch collection, without mention of type locality. Wermuth (1954) designated ZMB 278, a juvenile specimen from "Indien," as the lectotype of the species, thus fixing the type locality.

***Scincus carinatus* Schneider, 1801, *Hist. Amphib. II*: 183.**

Lectotype (here designated): ZMB 1253*, "ex India orientali," sent by John, probably from Tranquebar, to Bloch.

Current Name: *Mabuya carinata* (Schneider 1801).

Remarks: Peters (1864) identified ZMB 1253 as the Bloch specimen examined by Schneider. Schneider indicates explicitly that this specimen was sent to Bloch by John. Additional specimens in the collection of Lampe, and now presumed lost, constituted the remaining syntypes. Lampe was a surgeon from Hanover, whose collection passed to the museum of the University of Breslau in 1814. Gravenhorst (1851) reviewed Schneider's types from this collection and identified the material as belonging to *Mabuya trivittata* and *M. multifasciata*, as well as to *M. carinata* proper. Given the several species lumped under this name and the apparent loss of the remaining types, I take this opportunity to formally designate the surviving ZMB specimen as the lectotype of *Scincus carinatus*.

***Boa conica* Schneider, 1801, *Hist. Amphib. II*: 268.**

Syntype: ZMB 1470*, "ex India orientali" (Tranquebar), sent by John to Bloch.

Current Name: *Eryx conicus* (Schneider, 1801).

Remarks: Schneider noted explicitly that this specimen had been sent by John to Bloch. Although no specific locality was given in the description, Stimson (1969) reported "Tronquebar" as the type locality. This locality is indicated on the original label of the jar containing the type. A second syntype specimen, from the Museo Barbyensi, has not been traced.

***Boa anguiformis* Schneider, 1801, *Hist. Amphib. II*: 269.**

Syntype: ZMB 1460*, "ex India orientali."

Current Name: *Eryx johnii* (Russell, 1801).

Remarks: This is one of three specimens upon which Schneider's description was based. The specimen was listed as *Boa anguiformis* on the jar label but entered into the ZMB register as *Eryx johnii* from "Bengalen." Stimson (1969) indicated that the type had not been traced.

***Pseudoboa fasciata* Schneider, 1801, *Hist. Amphib. II*: 283.**

Syntypes: ZMB 2771-2, no locality given in description, but the ZMB catalogue indicates "Indien."

Current Name: *Bungarus fasciatus* (Schneider, 1801).

Remarks: Toriba (1993) indicated that the type had not been located.

***Pseudoboa caerulea* Schneider, 1801, *Hist. Amphib. II*: 284.**

Syntype: ZMB 2787*, "ex India orientali."

Current Name: *Bungarus caeruleus* (Schneider, 1801).

Remarks: Schneider's description is clearly based on two specimens, this one from the Bloch collection, and a second specimen from Vizagapatam illustrated by Russell (1801). Subsequent authors have accepted Vizagapatam as the type locality (e.g., Smith, 1943; Toriba, 1993) without comment. Toriba (1993) indicated that the type had not been located, but it is unclear if he was aware of the Berlin specimen, or was merely referring to the specimen figured by Russell (1801).

***Elaps bilineatus* Schneider, 1801, *Hist. Amphib.* II: 299.**

Syntypes: ZMB 2273, 2279, "ex India orientali," sent by John, probably from Tranquebar, to Bloch.

Current Name: *Amphiesma stolatum* (Linnaeus, 1758).

Remarks: Schneider specifically mentioned two specimens in the Bloch collection as the types. John, who had provided the specimens, presumably from Tranquebar, also provided Bloch with the local name for this snake: "komberumuken." John probably was attempting to represent the Tamil "komberi moorkan" which, however, is correctly applied to *Boiga ceylonensis*, *Dendrelaphis bifrenalis*, *D. caudolineolatus*, and *D. tristis* (see Das, 1998). According to Das (1998) there are several Tamil vernacular names for *A. stolatum*, but none are similar to "komberumuken."

***Typhlops oxyrhynchus* Schneider, 1801, *Hist. Amphib.* II: 341.**

Syntypes: ZMB 3825-6*, "ex India orientali," sent by John to Bloch.

Current Name: *Rhinophis oxyrhynchus* (Schneider, 1801).

Remarks: These two specimens were sent to Bloch by John, probably from Tranquebar. Gans (1966) identified these two specimens as the types, but considered them to be lost.

***Hydrus colubrinus* Schneider, 1799, *Hist. Amphib.* I: 238.**

Holotype: ZMB 9078*, no locality provided by Schneider

Current Name: *Laticauda colubrina* (Schneider, 1799).

Remarks: The data accompanying the specimen identify it as being from the "Ostindisches Meer," and as having come from the Lampe collection, most of which had been obtained by the museum of the University of Breslau early in the 19th Century. This specimen, given its relatively high catalogue number, must have been obtained, or at least accessioned, much later, during the directorship of Wilhelm Peters. This specimen has previously been identified as the type of *H. colubrinus* by McCarthy (1993).

***Otocryptis bivittata* Wiegmann, 1831, *Isis von Oken* 24: column 293.**

Holotype: ZMB 708*, no locality provided in description.

Current Name: *Otocryptis wiegmanni* Wagler, 1830.

Remarks: Although this specimen was marked in the ZMB register as lost, it was present during my examination of the collection. Wiegmann noted in the description that the specimen had come from the Bloch collection and Peters (1860b) remarked on this type when referring to specimens sent to Berlin by Schmarda. ZMB 708 is also the holotype of the senior synonym *Otocryptis wiegmanni* (Denzer et al., 1997). The citation for this description is often miscited as occurring on page 293 of the journal in which it was published. Many issues of the *Isis von Oken* were printed in double column format, with each column being sequentially numbered.

Several other Indian specimens from Bloch's collection are mentioned in Schneider's (1799, 1801) works, but not as types. Under his account of *Calamita cinereus* (= *Hyla cinerea*), Schneider (1799: 174) noted a similarly patterned frog from "India orientalis", and in his account of *Bufo viridis* (1799: 206), three Indian specimens sent by John are mentioned (these specimens could not be located and the true specific identity of these specimens is unknown). Schneider (1801:330) also mentioned two Bloch specimens of *Anguis maculatus* (= *Cylindrophis maculata*) that are extant as ZMB 1457-8*. Schneider (1801:199) noted numerous specimens of *Scincus punctatus* (= *Lygosoma punctata*) from India in Bloch's collection. At least two of these survived until the middle of the last century as ZMB 1204-5, although these specimens were not located in the museum inventory of 1967 or in my search of the collection. *Hydrus granulatus* (= *Acrochordus granulatus*) was described by Schneider (1799: 243) on the basis of a specimen from the Lampe collection. A skin sent to Bloch by John is also mentioned, but was excluded from the type description as Schneider was uncertain if it was conspecific with the Lampe type. No Bloch *Acrochordus* could be located in the Berlin collection during

my studies. Finally, a Bloch specimen of *Hydrus bicolor* (= *Pelamis platurus*) was examined by Schneider, but this specimen, of unstated locality, could not be located in the Berlin collection.

At least 15 other south Asian specimens from the Bloch Museum that were not discussed by Schneider (1799, 1801) are also represented in the ZMB collection. All except one, *Emys trijuga* (ZMB 106, lost) which is catalogued as being from Pondichery (and may be incorrectly catalogued as a Bloch specimens), bear only the locality "Ostindien." These are: *Crocodilus palustris* (ZMB 256*), *Gekko gecko* (ZMB 353*), *Hemidactylus triedrus* (ZMB 373*), *Calotes calotes* (ZMB 691–692*), *Calotes versicolor* (ZMB 695–6, lost), *Ahaetulla prasina* (ZMB 2392, 2397), *Atrietum schistosum* (ZMB 2054), *Boiga trigonata* (ZMB 2639), *Chrysopelea taprobanica* (ZMB 2559), *Dendrelaphis pictus* (ZMB 1608), *Enhydris enhydris* (ZMB 2508), *Homalopsis buccata* (ZMB 2507), *Lycodon aulicus* (1783 lost, 1784*, 1794–5*), and *Hypnale hypnale* (ZMB 2941). *Boiga trigonata* (as *Coluber trigonata*) was described by Schneider (Schneider in Bechstein, 1802), but of the three specimens mentioned in the description, only one figured by Russell (1796) can be unambiguously identified.

OTHER EARLY COLLECTIONS OF INDIAN HERPETOLOGICAL SPECIMENS

Although Bloch's collection is the single most important historical component of Berlin's south Asian herpetological collections, it is by no means the only one. Indeed, material from India and Sri Lanka continued to arrive in the museum throughout the first decades following its founding. In 1817, a number of Indian specimens reached Berlin through the purchase of the herpetological collection of Graf von Borcke auf Hueth for 2,500 Thaler (Peters, 1860a). Like Bloch's collection, von Borcke's was global in scope and greatly enriched Berlin's holdings. In 1822, for example, of 314 colubrids in the collection, 93 had come from Bloch's collection, and 86 from von Borcke's. The von Borcke specimens that could be identified are: *Hemidactylus leschenaultii* (ZMB 393), *Cylindrophis*

maculatus (ZMB 1453), *Amphiesma stolatum* (ZMB 2282), *Dendrelaphis pictus* (ZMB 1606–7), *Fordonia leucobalia* (ZMB 2245), *Homalopsis buccata* (ZMB 2506), *Lycodon aulicus* (ZMB 1799–1802), and *Naja naja* ZMB (2796, 2798).

Another important contributor was the Frenchman Lemarre-Picquot, from whom material was received into the Berlin collections in 1818, 1819, 1821, 1822, 1832, 1835, 1836, 1839, 1845, and 1846. The largest part of the collection was obtained in 1836, when an entire natural history collection, including 300 herpetological specimens, was acquired by the museum for 6,000 Thaler (Peters, 1860a). These included several aquatic species with the locality "Ganges" – *Hardella thurjii* (ZMB 111), *Aspideretes gangeticus* (ZMB 33), *Aspideretes hurum* (ZMB 32), and *Enhydrina schistosus* (ZMB 2831), and numerous specimens with the localities "Bengalen" – *Calotes versicolor* (ZMB 697–9), *Lygosoma albopunctata* (ZMB 1256), *Mabuya carinata* (ZMB 1254), *Chrysopelea ornata* (2560–1), *Dendrelaphis pictus* (ZMB 1604–5), *Lycodon aulicus* (ZMB 1790–2, 1803), *Xenochrophis piscator* (ZMB 2029–30), and *Bungarus caeruleus* (ZMB 2786), or the more general "Indien" or "Ostindien" – *Hardella thurjii* (ZMB 110), *Lissemys punctata andersoni* (ZMB 44*, 49634–5*), *Boiga trigonata* (ZMB 2638) and *Ptyas mucosus* (ZMB 1590). Lemarre-Picquot also provided a large collection of material to the Paris Museum (Duméril and Bibron, 1834), including some of the types of *Varanus picquotii*, named in his honour.

Substantial additional material was received from Delbrück (collections received by ZMB in 1820, 1822, 1823, 1824): *Eryx conicus* (ZMB 1463), *Eryx johnii* (ZMB 1459), both with the locality Pondicherry, *Acrochordus granulatus* (ZMB 1540) from "Indien," and *Hydrophis ornatus* (ZMB 2838*) from "Ind. Meer," von Orlich (who sent material from Calcutta in 1845, 1846, and 1856): *Cyrtodactylus pulchellus* (ZMB 425), *Hemidactylus leschenaultii* (ZMB 400 [2 specimens]), *Hemidactylus maculatus* (ZMB 375), *Calotes mystaceus* (ZMB 702), *Typhlops diardii* (ZMB 1417), *Acrochordus*

granulatus (ZMB 1541), and *Elaphe helena* (ZMB 1574), and Frederic John Mouat (1816–1897; Inspector General of Prisons of Bengal, and Professor of Chemistry, Medicine and Medical Jurisprudence, who sent material from Calcutta in 1853): *Varanus bengalensis* (ZMB 47), *Ramphotyphlops braminus* (ZMB 1419), *Chrysopelea ornata* (ZMB 2568, 39420), *Elaphe radiata* (ZMB 1740), *Lycodon aulicus* (ZMB 1806), and *Bungarus fasciatus* (2788). Smaller collections were received from Bengal from the missionary Ansorge, also based in Calcutta (material forwarded in 1857): *Aspideretes gangeticus* (ZMB 45, Ganges), *Amphiesma stolatum* (ZMB 3031), *Dendrelaphis pictus* (ZMB 3028), *Oligodon arnensis* (ZMB 2091), and *Bungarus caeruleus* (ZMB 2785) and Prince Waldemar of Prussia: *Uromastix hardwickii* (ZMB 824–5), and several other specimens were received without data, e.g., *Kachuga tecta* (ZMB 115 [2 specimens]), and *Rhabdophis subminiatus* (ZMB 2285–6).

The only older types derived from Indian collections, other than Bloch's (and the later-accessioned Lampe type of *Hydrus colubrinus*) were collected by Wilhelm Peters on his return trip from Africa. Peters left Mozambique on 7 August 1847 and was in Bombay on the 28th of September and in Sri Lanka (Kandy) on 4 December (Bauer et al., 1995). Apparently Peters stopped at Goa, probably before going to Bombay, having taken a Portuguese ship. Peters evidently collected little while in India, but two specimens, the type of *Eryx conicus* var. *laevis* and a *Hoplobatrachus tigerinus*, sent from Goa were recorded in the *ZMB Eingangs Journal 1811–1857*, with the indication that they did not arrive in Berlin until September 1849, more than a year after Peters himself returned via Egypt. At least two other specimens, the types of *Emyda vittata*, were also collected at the same time. Although the frog noted above could not be located in the Berlin collection, Peters' types are extant.

Emyda vittata Peters, 1854, *Ber. Bekanntmach. Geeignet. Verhandl. Königl.-Preuss. Akad. Wiss. Berlin* 1854: 216.

Syntypes: ZMB 46*, 17772*, "India orientalis, Goa," collected by Wilhelm Peters in late 1847.

Current Name: *Lissemys punctata* (Bonnaterre, 1789).

Remarks: These types were discussed by Fritz et al. (1994).

Eryx conicus var. *laevis* Peters, 1869, *Mber. Königl.-Preuss. Akad. Wiss. Berlin* 1869: 436.

Holotype: ZMB 1469*, "bei Goa," collected by Wilhelm Peters in late 1847.

Current Name: *Eryx conicus* (Schneider, 1801).

Remarks: Peters' name was not included in Stimson's (1969) review of the taxonomy of the species.

A final source of early south Asian herpetological material in Berlin was through institutional exchanges. These included fairly large transfers of specimens from Paris, made through Achille Valenciennes in 1837, 1840, and 1851, and Leiden, made through Hermann Schlegel in 1849 and earlier though Coenraad Temminck, as well as smaller exchanges from the museums in Munich and Vienna. Extant material obtained through this means includes *Tomopterna breviceps* (ZMB 3352–3) and *Xenochrophis piscator* (ZMB 2031) from Leiden, *Elaphe helena* (ZMB 1575) from Vienna, and *Calotes versicolor* (ZMB 714[2 specimens]) from Bombay from Munich. Paris provided specimens of *Sitana ponticeriana* (ZMB 710), *Atrietum schistosum* (ZMB 2038 Ostindien), and *Ptyas mucosus* (ZMB 1591), as well as a syntype of *Hemidactylus maculatus* Duméril and Bibron 1836 (ZMB 374) from "Bengalen, Ost-Indien" (Bauer and Günther, 1991).

HERPETOLOGICAL COLLECTIONS FROM SRI LANKA

Collections from Sri Lanka arrived in Berlin later than those from India, chiefly after 1845, but included important specimens, many of which were subsequently described as new. Such material was sent to Berlin by Werner Hoffmeister and Prince Waldemar of Prussia (in 1845 and 1847), Johann Nietner (in 1854–56),

and Ludwig Karl Schmarda (in 1855–57), as well as a few specimens from other collectors, including Cuming (*Boiga ceylonensis*, ZMB 3732).

Of Hoffmeister's material, apparently initially consisting of only seven specimens of amphibians and reptiles, three specimens could be traced during the course of my study. These are ZMB 2027, a specimen of *Xenochrophis piscator* with the locality "Ceylon," and two type specimens:

***Ixalus leucorhinus* Lichtenstein and von Martens, 1856, *Nomencl. Rept. Amphib.* 36.**

Holotype: ZMB 3057*, "Ceylon," collected by W. Hoffmeister.

Current Name: *Philautus leucorhinus* (Lichtenstein and von Martens, 1856).

Remarks: Frost (1985) indicated that the type was in Berlin, but did not provide the specimen number.

***Ixalus poecilopleurus* Lichtenstein and von Martens, 1856, *Nomencl. Rept. Amphib.* 36.**

Holotype: ZMB 3058*, "Ceylon," collected by W. Hoffmeister.

Current Name: *Theloderma schmarda* (Kelaart, 1854).

Johann Nietner's contributions to natural history were chiefly as an entomologist, however, he made general collections and provided the Zoological Museum in Berlin with numerous herpetological specimens, including the types of five taxa, described both by Lichtenstein and von Martens and by Peters. All of these types were identified during recent examinations of the ZMB collections:

***Hemidactylus pustulosus* Lichtenstein and von Martens, 1856, *Nomencl. Rept. Amphib.* 5.**

Holotype: ZMB 388*, "Ceylon," collected by J. Nietner.

Current Name: *Hemidactylus leschenaultii* Duméril and Bibron, 1836.

Remarks: This type was referred to by Bauer and Günther (1991).

***Cophotis Ceylanica* Peters, 1861, *Mber. Königl.-Preuss. Akad. Wiss. Berlin* 1861: 1103.**

Lectotype: (designated by Marx 1958, by implication) ZMB 4240*, "Ceylon," collected by J. Nietner.

Remarks: FMNH 73844 is a paralectotype. Bauer et al. (1995) suggested that ZMB 8428 (3 specimens) and 8429 (3 specimens) might also be paralectotypes, but Peters clearly indicated that there were only two specimens in the type series.

***Hydrophis bituberculatus* Peters, 1873, *Mber. Königl.-Preuss. Akad. Wiss. Berlin* 1873: 855; plate 2 (fig. 2).**

Holotype: ZMB 4647*, "Colombo (Ceylon)," collected by J. Nietner.

Remarks: McCarthy (1993) cited this specimen as the holotype.

***Polypedates biscutiger* Peters, 1871: 649.**

Syntypes: ZMB 3045* (2 specimens), 3046*, 3047* (2 specimens), 3048 (2 specimens), 3049–50 (not located).

Type locality: "Rambodde (Ceylon)" (Ramboda, Sri Lanka).

Current Name: *Rhacophorus maculatus biscutiger* (Peters, 1871) fide Dubois (1986). This identification has been questioned, however, and the syntypes may in fact be referable to *Polypedates eques* Günther 1859 (R. Pethiyagoda, pers. comm.).

Remarks: Dubois (1986) regarded the syntype series as consisting of only three specimens.

***Rana corrugata* Peters, 1863: 412.**

Syntypes: ZMB 4897* (3 specimens), "Rambodde auf Ceylon" (Ramboda, Sri Lanka), collected by J. Nietner.

Current Name: *Limnonectes corrugatus* (Peters, 1863).

Remarks: Frost (1985) indicated that the type was in Berlin, but did not cite this specimen.

Other specimens from Nietner came from Rambodde: *Hemidactylus triedrus* (ZMB 372), *Lygosoma albopunctata* (ZMB 1218), *Lygosoma punctata* (ZMB 1351), and *Elaphe helena* (ZMB 1573), or merely from "Ceylon": *Limnonectes* sp. (ZMB 3275), *Rana malabaricus* (ZMB 3253), *Polypedates cruciger* (ZMB 3044), *Calotes calotes* (ZMB 690, 693), *Calotes versicolor* (ZMB 700), *Ramphotyphlops braminus* (ZMB 1418), *Cylindrophis maculata* (ZMB 1456[2 specimens]), *Amphiesma stolatum* (ZMB 2273), *Boiga ceylonensis* (ZMB

2028), *Cercaspis carinata* (ZMB 1815), *Dendrelaphis tristis* (ZMB 1609), *Lycodon aulicus* (ZMB 1807), *Oligodon arnensis* (ZMB 2089), *Xenochrophis piscator* (ZMB 2028), *Pelamis platurus* (ZMB 2825[3 specimens]), and *Trimeresurus trigonocephala* (ZMB 2982, 2986*).

Ludwig Karl Schmarda (1819–1908) was an Austrian, born in Olmütz (now Olomouc, Czech Republic), who was a university professor in Graz, Prague and Vienna, and was strongly interested in zoogeography. His collections were made during 1853–57 during a research trip around the world. Peters (1860b) provided a list of 41 species from Sri Lanka given by Schmarda to the museum, among them were two types, one of which is in Berlin. The second type, that of *Calotes (Bronchocele) nigrilabris* from “Newera Ellia” (= Nuwara Eliya), is represented only by the holotype in Vienna, NMW 23355 (Tiedemann et al., 1994; Bauer et al., 1995). The material collected by Schmarda came from several localities: Trinkomalie (= Trinomalee) (*Hemidactylus leschenaultii* ZMB 3006, 3013; *Otocryptis wiegmanni vittata* ZMB 3004 [2 specimens], 3008 [2 specimens]), Ratnapura (*Theloderma schmarda* ZMB 3059), Galle, Hinidu, Newera Ellia (= Nuwara Eliya) (*Aspidura trachyprocta*, ZMB 3035), Adams Pic (= Adam’s Peak), and Kandy, and also included material without specific locality (*Nessia burtonii* ZMB 3017): Peters described a third type from the material in 1863.

***Hoplobatrachus ceylanicus* Peters, 1863, Mber. Königl.-Preuss. Akad. Wiss. Berlin 1863: 449.**

Holotype: ZMB 3354*, “Trinkemalie, Ceylon” (Trincomalee, Sri Lanka), collected by L. K. Schmarda.

Current Name: *Hoplobatrachus crassus* (Jerdon, 1853).

Remarks: Bauer et al. (1995) indicated that the type was not located. I have since determined that the type is ZMB 3354, which had been catalogued as *Pyxicephalus fodiens*, a name that Peters used to refer to the specimen in an 1860 publication.

***Lygosoma fallax* Peters, 1860, Mber. Königl.-Preuss. Akad. Wiss. Berlin 1860: 184.**

Syntype: ZMB 3762*, “Ratnapura, Trinkomalie” (= Trincomalee), collected by L. K. Schmarda.

Current Name: *Lankascincus fallax* (Peters, 1860).

Remarks: Greer (1991) regarded the ZMB specimen as the holotype. Tiedemann et al. (1994) listed NMW 16630: 1–9 as additional types. It is not clear if the NMW specimens were part of the type series and their status as syntypes is questionable; however, Peters’ description implies more than one specimen in the type series.

LICHTENSTEIN’S “DOUBLETEN”

Another type of published information regarding south Asian specimens in the Berlin collection are the catalogues of “Doubletten” or duplicate specimens published by Lichtenstein in order to raise money for the museum and finance the purchase of new collections. Lichtenstein (1823) in his first major catalogue of duplicate specimens cited a number of specimens from “India orientalis,” some of which may have come from the Bloch collection, although this is difficult to verify. In all, ten such taxa were listed. Of these, only five actually occur in south Asia: *Agama colotes* (= *Calotes calotes*), *Gekko teres* (= *Gekko gekko*), *Scincus punctatus* (= *Lygosoma punctata*), *Scincus carinatus* (= *Mabuya carinata*), and *Ilysia maculata* (= *Cylindrophis maculatus*). Another four are south-east Asian: *Gekko vittatus* (= *Gekko vittatus*), *Acrochordus javanicus*, *Ilysia rufa* (= *Cylindrophis ruffus*), and one, *Monitor saurus* (= *Varanus niloticus*) is African.

Lichtenstein continued to list “Doubletten” for sale for the rest of his directorship (1811–1857), but the majority of items for sale were birds. Nonetheless, herpetological items occasionally were also sold, including specimens from the collections of Bloch, Hemprich and Ehrenberg (Middle East and North Africa), and Wilhelm Peters (Mozambique) (see Mauersberger, 1988 for a list of all of the speci-

men sales). The last such catalogue was the *Nomenclator* of 1856 which has usually been ascribed to Lichtenstein (e.g., Bauer and Günther, 1991), or Lichtenstein and von Martens (e.g., Harris and Kluge, 1984). Lichtenstein, who authored the introduction to this work, noted that Christoph David Friedrich Weinland had begun the work of the *Nomenclator*, but that the editing and completion of the work was accomplished by Lichtenstein himself and Eduard Carl von Martens. In most of his own papers, Peters did not ascribe the names described therein to any particular author, rather authorship was cited only as "*Nomenclator rept. et amph. Mus. Berol.*" or just "*Mus. Berol.*," however, late in life (Peters, 1882) he referred to names having been published "In dem von den Herren Dr. Weinland und v. Martens bearbeiteten *Nomenclat. Reptil. et Amphib. Mus. Berol.* 1856." Unfortunately, this still leaves open the question of the authorship of new names, which may in fact have been the work of any one or more of the authors. In this paper I have attributed names to Lichtenstein and von Martens, but further investigation of this issue is required.

Peters (1863a) in many ways regarded the *Nomenclator* as a disaster, citing numerous errors therein, including major errors of locality for some of the new species described. In total, 96 taxa with the general locality "Ostindien" or more specific south Asian localities (e.g., Ganges, Calcutta, Pondicherry, Dekan, Bengalen, Goa, Ceylon) were listed. Omitting extralimital taxa (mostly south-east Asian) and those with obviously incorrect locality data, the following 72 names, representing 65 recognizable south Asian taxa were listed in the *Nomenclator* (each listed in the order in which it appeared, followed by the current name, if different, in square brackets and the locality given in the *Nomenclator* in parentheses): **Testudines:** *Trionyx ocellatus* [*Aspideretes hurum*] (Ganges), *Cryptopus granosus* [*Lissemys punctata*] (Ostindien), *Emys trijuga* [*Melanocheilus trijuga*] (Pondicherry), *Emys Hamiltonii* [*Geoclemys hamiltonii*] (Ganges), *Emys Thurgyi* [*Hardella thurjii*] (Ganges), *Emys tectum* [*Kachuga tecta*] (Ganges). **Crocodylia:** *Gavialis gangeticus* (Ganges).

Lacertilia: *Chamaeleon vulgaris* var. b. [*Chamaeleo zeylanicus*] (Indien?), *Platydictylus Duvaucelii* [?, non *Hoplodactylus duvaucelii* Duméril and Bibron 1836] (Calcutta), *Hemidactylus triedrus* (Ostindien), *Hemidactylus maculatus* (Ostindien), *Hemidactylus pustulosus* [*Hemidactylus leschenaultii*] (Ceylon), *Hemidactylus frenatus* (Calcutta), *Hemidactylus marginatus* [*Cosymbotus platyurus*] (Calcutta), *Gymnodactylus pulchellus* [*Cyrtodactylus pulchellus*] (Calcutta), *Varanus bengalensis* (Calcutta), *Calotes ophiomachus* [*Calotes calotes*] (Zeilon), *Calotes versicolor* (Bengal, Zeilon), *Calotes mystaceus* (Calcutta), *Calotes pictus* [?] (Dekan), *Lyriocephalus scutatus* (Ostindien), *Otocryptis bivittata* [*Otocryptis wiegmanni*] (Ostindien), *Ceratophora Stoddaertii* [*Ceratophora stoddartii*] (Ceylon), *Sitana pondiceriana* [*Sitana ponticeriana*] (Ostindien), *Uromastix Hardwickii* [*Uromastix hardwickii*] (Ostindien), *Eumeces punctatus* [*Lygosoma punctata*] (Ostindien), *Euprepes carinatus* [*Mabuya carinata*] (Bengalen). **Serpentes:** *Pilidion* sp. [*Typhlops* sp. (Calcutta), *Typhlops nigroalbus* [*Typhlops diardii*] (Calcutta), *Typhlops braminus* [*Ramphotyphlops braminus*] (Calcutta, Ceylon), *Rhinophis oxyrhynchus* (Ceylon), *Rhinophis punctatus* (Ostindien?), *Cylindrophis maculatus* (Ostindien), *Eryx Johnii* (Bengalen, Pondicherry), *Eryx conicus* (Goa), *Python molurus* (Ostindien), *Python reticulatus* (Ostindien), *Acrochordus javanicus* [*Acrochordus granulatus*] (Calcutta), *Chersydrus granulatus* [*Acrochordus granulatus*] (Ostindien), *Oligodon sublineatum* [*Oligodon sublineatus*] (Ceylon), *Oligodon subpunctatum* [*Sibynophis sagittarius*] (Ostindien), *Coluber mucosus* [*Ptyas mucosus*] (Bengalen), *Tropidonotus palustris* [*Xenochrophis piscator*] (Bengalen, Ceylon), *Tropidonotus schistosus* [*Atridium schistosum*] (Ostindien), *Coronella* sp. [?] (Ceylon), *Simotes Russelii* [*Oligodon arnensis*] (Ceylon), *Plagiodon Helena* [*Elaphe helenae*] (Bengalen), *Dendrophis pictus* [*Dendrelaphis pictus*] (Bengalen, Ceylon), *Campsosoma radiatum*

[*Elaphe radiata*] (Calcutta), *Lycodon aulicum* [*Lycodon aulicus*] (Calcutta), *Amphiesma stolatum* [*Amphiesma stolatum*] (Bengalen, Ceylon), *Dryophis prasinus* [*Ahaetulla prasina*] (Calcutta), *Cerberus boaeformis* [*Cerberus rynchops*] (Bengalen), *Chrysopelea ornata* (Calcutta), *Dipsas trigonata* [*Boiga trigonata*] (Ostindien), *Hydrophis schistosa* [*Enhydrina schistosus*] (Gangesmündungen), *Bungarus fasciatus* (Calcutta), *Bungarus lineatus* [*Bungarus caeruleus*] (Bengalen), *Naja tripudians* [*Naja naja*] (Bengalen, Pondichery, Ceylon), *Echidna elegans* [*Daboia russelii*] (Ostindien), *Trigonocephalus Hypnale* [*Hypnale hypnale*] (Ostindien). **Anura:** *Polypedates leucomystax* [*Polypedates* sp.] (Ceylon), *Polypedates rugosus* [*Polypedates* sp.] (Ceylon), *Ixalus leucorhinus* [*Polypedates maculatus*] (Ceylon), *Ixalus poecilopleurus* [*Theloderma schmarda*] (Ceylon), *Rana Leschenaultii* [*Uperodon systoma*] (Ostindien), *Rana malabarica* (Ostindien), *Rana tigrina* [*Hoplobatrachus tigerinus*] (Goa, Ceylon), *Rana macrodon* [*Limnonectes* sp.] (Ceylon), *Pyxicephalus fuscimaculatus* [?](Bengalen, Dekan), *Engystoma ornatum* [*Microhyla ornata*] (Dekan, Ceylon), *Hyperodon marmoratum* [*Uperodon systoma*] (Ostindien).

Three of the taxa listed, *Ixalus leucorhinus*, *Ixalus poecilopleurus*, and *Hemidactylus pustulosus*, all from Sri Lanka, were described in the *Nomenclator* as noted above. Aside from these types, it is often difficult to match the specimens listed in the *Nomenclator* with known numbered specimens, because no numbers were provided in the *Nomenclator*, the identifications given in 1856 may be incorrect, or because the wrong localities may have been associated with some specimens (see Peters, 1863a). However, some can be identified because of their locality. Thus, the few specimens from Goa are those collected by Peters, and those from "Dekan" were specimens received from the Leiden Museum as exchanges.

LATER SOUTH ASIAN MATERIAL IN THE BERLIN COLLECTION

For much of the rest of Peters' career, additional south Asian material entered the ZMB collection. After the 1850's, however, much of this material was obtained by way of exchanges from other institutions. In particular, a great deal of material appears to have been received from the Asiatic Society of Bengal, in Calcutta. This included many uropeltids, many of which were used by Peters (1859, 1861a, 1861c) in preparing his revisionary works on this group, as well as representatives of many of the species of amphibians and reptiles described by Blanford, Anderson, Jerdon, and especially Beddome. Included in this number are many specimens that are known or believed to be part of type series (see Bauer and Günther, 1991; Bauer et al., 1993; Fritz et al., 1994). At least some of these specimens were sent to ZMB from Beddome via Oldfield Thomas at the BMNH in 1881 (Bauer and Günther, 1991), but others had been arriving over time since the late 1850's. These specimens expanded the geographic scope of the Berlin Museum's holdings to include much of south India, as well as parts of Pakistan and north India. Other specimens, again including syntypes, were also obtained from Albert Günther at the British Museum, and from Paris. Fittingly, one of the specimens obtained from the latter institution was a syntype of *Varanus picquotii* Duméril and Bibron 1836 [*V. flavescens*] (ZMB 7014, now lost), collected by Lemarre-Picquot from "Bengale" (Good et al., 1993).

CONCLUSIONS

Although the modern perception of early Indian and Sri Lankan systematic herpetology emphasizes the role of British workers in the field, it is clear that zoologists of other nationalities were also active in this part of the world. Indeed, the collections of Marcus Bloch in Berlin must have been among the most extensive Indian holdings in Europe in the 1790's. That much of Bloch's material is extant in Berlin appears to be unknown to many modern workers, who have tended to be ignorant of the collection or to underestimate its historical value. This has been ex-

acerbated by the fact that Schneider's descriptions of this material were published in Latin, a language no longer understood by most systematists. South Asian material obtained and described by later workers and present in Berlin has also frequently been ignored by recent workers. However, both the richness of the Indian and Sri Lankan ZMB type holdings and the diversity of the general collections from this region obtained by the museum during the period 1810–1857 clearly attest to the significance of the Zoological Museum, Berlin as a repository of specimens of both taxonomic and historical importance. Bauer et al. (1995) attempted to dispel the misapprehension that most of the type specimens designated by Wilhelm Peters had been lost or destroyed during World War II; the data presented herein clearly establish that the collections, including types, predating Peters' era at the museum have also survived and that the Berlin Museum should be considered as one of the most important European repositories of early south Asian herpetological material.

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CATALOGUE OF HERPETOLOGICAL TYPES IN THE COLLECTION OF THE BOMBAY NATURAL HISTORY SOCIETY

Indraneil Das¹ and Naresh Chaturvedi²

¹Institute of Biodiversity and Environmental Conservation, Universiti Malaysia Sarawak,
94300 Kota Samarahan, Sarawak, East Malaysia.

Email: idas@mailhost.unimas.my

²Bombay Natural History Society, Hornbill House,
Shaheed Bhagat Singh Road, Mumbai 400 023, India.

Email: bnhs@bom3.vsnl.net.in

ABSTRACT.- The herpetological types of the Bombay Natural History Society, Bombay (now Mumbai), India, are listed, current to 11 October, 1998. The collection includes historical specimens collected by Major Frank Wall, from India, Myanmar (formerly Burma) and Iran, as well as those described more recently. The annotated list includes original citations, registration numbers, nature of type and present status of every taxa, with additional remarks where necessary. In all, 24 primary and secondary types are present, including 21 name-bearing taxa (including three Anura, three Sauria and 13 Serpentes). The provenance of the types include localities in China, India, Iran and Myanmar (Burma). A list of types that were not located, in addition to those erroneously mentioned as being in the collection, is included.

KEY WORDS.- Bombay Natural History Society, amphibians, reptiles, type specimens, type catalogue.

INTRODUCTION

The Bombay Natural History Society was established informally by seven men (D. McDonald, E. H. Aitken, C. Swinhoe, J. C. Anderson, J. Johnston, A. Pandurang, G. A. Maconochie and S. Arjun), who met in the rooms of the Victoria and Albert Museum at Byculla, Bombay for the first time on 15 September, 1883 (Anon., 1983a; 1983b; Hawkins, 1983). Although the initial objectives of the Society were to “meet monthly and exchange notes, exhibit interesting specimens and otherwise encourage each other” (Anon., 1983a), the Society swiftly grew in terms of both membership and reputation, to become one of the best known natural history societies in the world (Anon., 1983e). Its natural history collections, while mostly confined to the Indian region (including Sri Lanka and Myanmar), also have representatives from extralimital areas, and while the herpetological collections are not at par with those of mammals, birds and butterflies, they contain many historical specimens, including types of both amphibians

and reptiles. Important donors of material include Reverend Fr. Dreckman and H. Phipson and, especially, Major Frank Wall (Anon., 1983c).

Although the natural history collections were first housed at 6, Apollo Street (now Shahid Bhagat Singh Road), Phipson’s appointment by the Government to the Committee set up in 1904 to consider the question of a public museum for Bombay led, in 1921, to the establishment of the Prince of Wales Museum, where the collections were transferred (Anon., 1983d).

The original descriptions of most of the new species based on the Bombay Natural History Society collections have been published in the *Journal of the Bombay Natural History Society*, a peer-reviewed periodical that was first published in 1886 (Anon., 1983f). Important herpetological papers to be published include the 29-part series on the common Indian snakes by Major Wall, each illustrated with exquisite water colours (a selection of which has since been re-

printed in a book on Indian reptiles by Daniel, 1983).

This paper provides an inventory of the herpetological types in the collection of the Bombay Natural History Society, as of 16 September, 1998. For every name-bearing type, the original name (retaining the original orthography), authority, with reference, the registration number and nature of the types, type locality (within quotes, when taken from the original description; without quotes, if this information is based on museum catalogue or other data), the current systematic status, and where appropriate, additional remarks, are provided. Institutional acronyms follow Leviton et al. (1985), which abbreviates the present collection as BNHM. In all, 24 primary and secondary types are represented, including eight holotypes, nine syntypes, six paratypes and one neotype, representing 21 name-bearing taxa (including three Anura, two Sauria and 15 Serpentes). In addition, types of nine name-bearing taxa (one lizard and eight snakes) are at present untraceable in the collection.

ANURA

BUFONIDAE

Bufo sulphureus Grandison & Daniel, 1964. *J. Bombay nat. Hist. Soc.* 61: 192.

Type: BNHM 377 (holotype), from "approximately 4000 ft. near Humbelevi village Koyna, Satara District, Maharashtra" (in western India).

Current status: Subjective synonym of *Bufo koyanensis* Soman, 1963.

RANIDAE

Nyctibatrachus humayuni Bhaduri & Kripalani, 1955. *J. Bombay nat. Hist. Soc.* 52(4): 852.

Type: BNHM 577/427/429 (paratype), from "Mahableshwar, Satara District, Bombay" (in Maharashtra State, western India). The paratype is registered as from Khandala (in Maharashtra State, western India).

Current status: *Nyctibatrachus humayuni* (Bhaduri & Kripalani, 1955).

Remarks: The holotype is ZSI 20628 (see also Frost, 1985).

RHACOPHORIDAE

Polypedates pseudocruciger Das & Ravichandran, 1998. *Hamadryad* 22(2): 89.

Types: BNHM 2863, from "Maramalai (08° 11'N; 77° 29'E), Kanyakumari District, Tamil Nadu State, southern India"; BNHM 2887, from "Coondapur (13° 38'N; 74° 42'E), Dakshin Kannada District, Karnataka State, south-western India" (both paratypes).

Current status: *Polypedates pseudocruciger* Das & Ravichandran, 1998.

Remarks: The species has been referred to *Polypedates cruciger* Blyth, 1852, in the literature.

SAURIA

EUBLEPHARIDAE

Eublepharis macularius fuscus Börner, 1981. *Saurológica, Cologne* (3): 4.

Type: BNHM 1047 (neotype), from "Hingolgaadh, Jasdan, Rajkot, Gujarat, India".

Current status: *Eublepharis fuscus* Börner, 1981.

Remarks: Elevated to species status by Das (1997), who designated the neotype.

GEKKONIDAE

Cyrtodactylus aravallensis Gill, 1997. *J. Bombay nat. Hist. Soc.* 94(1): 122.

Type: BNHM 1433 (holotype), from "Delhi Ridge...Jawaharlal Nehru Campus" (in northern India).

Current status: *Cyrtodactylus aravallensis* Gill, 1997.

Hemidactylus albofasciatus Grandison & Soman, 1963. *J. Bombay nat. Hist. Soc.* 60: 322.

Type: BNHM 148 (paratype), from "Dorle village, Rajapur Taluka, Ratnagiri District, Maharashtra" (in western India). The localities of the paratypes in the original description are "Dorle village, Rajapur Taluka, Ratnagiri District, Maharashtra...Dabhil village, Taluka and District Ratnagiri, Maharashtra...Gavkhadi village, Rajapur Taluka, Ratnagiri District..".

Current status: *Teratolepis albofasciatus* (Grandison and Soman, 1963).

Remarks: BMNH 74.4.29.1038-40 is the holotype, additional paratypes being at the BMNH 74.4.29.1038-40 (holotype), "Dorle village, Rajapur Taluka, Ratnagiri District, Maharashtra" (in India); BMNH 82.4.14.22 (paratype); "S. Canara" (in India) in the catalogue; ZSI 21109-12 (see Das et al., 1998).

SERPENTES UROPELTIDAE

Uropeltis macrolepis mahableshwarensis Chari, 1955. *J. Bombay nat. Hist. Soc.* 52(4): 901.

Type: BNHM 1994 (holotype), "Mahableshwar, ca. 4,500 ft., Satara District, Bombay State" (at present in Maharashtra State, western India).

Remarks: Several other specimens were examined, but none are apparently part of the type series.

Current status: *Uropeltis macrolepis mahableshwarensis* Chari, 1955.

COLUBRIDAE

Coluber leonardi Wall, 1921. *J. Bombay nat. Hist. Soc.* 28(1): 43.

Type: BNHM 466 (holotype), from "Sinlum Kaba, Burma, Lat. 24° Long. 97° at an elevation of 6,000 feet" (at present Myanmar).

Current status: *Elaphe leonardi* (Wall, 1921).

Contia zebrina Wall, 1923. *J. Bombay nat. Hist. Soc.* 29(3): 772.

Type: BNHM 768 (entry number 171-1) (holotype), from "Bazdad, South Persia" ('Bazdad' unlocated on maps and gazeteers consulted, and may be a typographical error for Baghdad in Iraq, which was on the travel route to south-western Iran in the early part of the century; S. C. Anderson, pers. comm., 1998).

Current status: Subjective synonym of *Pseudocyclophiops persicus* (Anderson, 1872).

Dendrophis gorei Wall, 1910. *J. Bombay nat. Hist. Soc.* 19(4): 829, 1 pl.

Types: BMNH 1946.1.10.30 (holotype), "Jaipur (Namsang)" (in Assam State, north-eastern India).

Remarks: The location of the paratype from "...near Dibrugarh (Atabari)" is unknown.

Current status: *Dendrelaphis gorei* (Wall, 1910).

Dryophis prasinus var. *flavescens* Wall, 1910. *J. Bombay nat. Hist. Soc.* 19(4): 834.

Types: The taxon was based on six syntypes from "Dibrugarh" (in eastern Assam State, north-eastern India), "Sadiya" (in eastern Assam, north-eastern India), near "Jaipur" (in eastern Assam, north-eastern India), "North Lakhimpur (Dejoo and at foot of Duffla Hills)" (in eastern Assam, north-eastern India). Only a single syntype, BNHM 1976, from North Lakhimpur is known to be extant, but others may, in fact, exist.

Current status: Subjective synonym of *Ahaetulla prasina* (Boie, 1827).

Remarks: Smith (1943: 375) erroneously attributes the authorship to Smith (1915: 785), citing the type locality as "Trang Pen. Siam".

Oligodon mcdougalli Wall, 1905. *J. Bombay nat. Hist. Soc.* 16(2): 251.

Type: BNHM 963 (holotype), from "Sandarang, Burma" (sic for Sandoway, according to Smith, 1943: 234; at present Thandwe, in Myanmar).

Current status: *Oligodon mcdougalli* Wall, 1905.

Remarks: Smith (1943) wrote that the type is lost, but Dowling and Jenner (1989) discovered the type in the BNHM collection.

Oligodon melaneus Wall, 1909b. *J. Bombay nat. Hist. Soc.* 19(2): 349.

Type: BNHM Unregistered (syntype), in Jar 61-5-958, from "Tindharia" (in northern West Bengal State, eastern India).

Current status: *Oligodon melaneus* Wall, 1909b.

Remarks: The second syntype is BMNH 1946.1.3.11.

Tarbophis tessellatus Wall, 1908b. *J. Bombay nat. Hist. Soc.* 18(4): 802.

Type: BNHM 2665 (holotype), "Maidan Mihaftan 30 m. E. of Shushtar in S. W. Persia...between the Zagros mountains and the vast plains of Persian Mesopotamia" (likely to be Maidan-i-Naftun, now encompassed by the town of Masjed Soleyman, Iran, according to S. C. Anderson, pers. comm., 1998).

Current status: *Telescopus tessellatus* (Wall, 1908b).

Remarks: A second specimen, BNHM 2666, bears the same collection data.

***Tropidonotus baileyi* Wall, 1907a. *J. Bombay nat. Hist. Soc.* 17(3): 617.**

Types: BNHM 1601-02 (syntypes), from "Thibet" (sic for Tibet, at present Xizang Autonomous Region, China).

Current status: *Thermophis baileyi* (Wall, 1907a).

Remarks: Assigned to the genus *Thermophis* by Malnate (1953); see also Zhao and Adler (1993: 261). Wall (1907a) mentioned that the species was described on the basis of 22 specimens; the fate of the rest of the syntypes is unknown.

***Tropidonotus venningi* Wall, 1912. *J. Bombay nat. Hist. Soc.* 20(2): 345.**

Types: BNHM 1316 (syntype), from "Haka Chin Hills" (in northern Myanmar).

Current status: *Amphiesma venningi* (Wall, 1912).

Remarks: A second syntype is in the BMNH. A third specimen was examined by Wall (1910a), which was not made part of the type series. According to the catalogue, BNHM 1316-1320 were collected by Capt. F. E. Venning.

ELAPIDAE

***Bungarus walli* Wall, 1907. *J. Bombay nat. Hist. Soc.* 17(3): 608; 1 pl.**

Type: BNHM 2169 (syntype), from "Fyzabad" (= Faizabad, Uttar Pradesh, northern India).

Current status: *Bungarus sindanus walli* Wall, 1907.

Remarks: Additional syntypes are BMNH 1946.1.18.51-53 and ZSI 5727 (see Das et al., 1998). Wall (1907) established the taxon on eight syntypes; the location of three of these are unknown.

***Callophis maclellandii* var. *gorei* Wall, 1909. *J. Bombay nat. Hist. Soc.* 19(4): 842.**

Type: BNHM 2211, from "Jaipur" (in Assam State, north-eastern India), is assumed here to be a syntype.

Current status: Subjective synonym of *Calliophis maclellandii* (Reinhardt, 1844).

Remarks: A second syntype is in the BMNH. The fate of the third syntype is unknown.

***Dendraspis hannah brunnea* Deraniyagala, 1961. *Spolia Zeylanica* 29(2): 229.**

Type: BNHM 2577 (paratype), "Tindharia near Darjeeling" (in northern West Bengal State, eastern India).

Current status: Subjective synonym of *Ophiophagus hannah* (Cantor, 1836).

Remarks: The holotype is ZSI 8924 (see Das et al., 1998).

VIPERIDAE

***Ancistrodon millardi* Wall, 1908a. *J. Bombay nat. Hist. Soc.* 18(4): 792.**

Types: The species was based on five syntypes from "Castle Rock" (in southern Maharashtra State, western India) and "Carwar" (= Karwar, western Karnataka State, western India). Two of the four syntypes from the second locality (BNHM 2531-32) are known to be extant.

Current status: Subjective synonym of *Hypnale hypnale* (Merrem, 1820).

***Trimeresurus huttoni* Smith, 1949. *J. Bombay nat. Hist. Soc.* 48(3): 596.**

Type: BNHM 2658 (paratype), "The High Wavy Mountains, Madura District, South India; altitude 5,200 feet" (a plateau in the western central edge of the Varushanad Hills, just east of Kambam, District of Madurai, State of Tamil Nadu, India, 1590 m).

Remarks: Transferred to the genus *Tropidolaemus* by David and Vogel (1998). The holotype is BMNH 1948.1.8.75.

Current status: *Tropidolaemus huttoni* (Smith, 1949).

TYPES NOT EXTANT IN THE BNHM
The following types are either lost or erroneously reported as being in the collection of the BNHM:

LACERTIDAE

***Acanthodactylus fraseri* Boulenger, 1918. *J. Bombay nat. Hist. Soc.* 25(3): 373.**

Types: Two syntypes supposedly in the BNHM, from "Zobeir, Lower Mesopotamia" (= Az Zubayr, Iraq), are untraceable.

Current status: Subjective synonym of *Acanthodactylus grandis* Boulenger, 1909.

SERPENTES TYPHLOPIDAE

***Typhlops wilsoni* Wall, 1908b. *J. Bombay nat. Hist. Soc.* 18(4): 796.**

Type: The holotype was in the collection of the BNHM at the time of description, from "Maidan Mihaftan 30 m. E. of Shushtar in S. W. Persia...between the Zagros mountains and the vast plains of Persian Mesopotamia" (likely to be Maidan-i-Naftun, now encompassed by the town of Masjed Soleyman, Iran, according to S. C. Anderson, pers. comm., 1998), but is untraceable at present, as reported by Hahn (1980: 76)..

Current status: *Typhlops wilsoni* Wall, 1908b.

COLUBRIDAE

***Dipsadomorphus jollyi* Wall, 1914. *J. Bombay nat. Hist. Soc.* 23(1): 167.**

Type: Lost, according to Smith (1943: 360), from "Kacha Thana, Baluchistan" (in north-western Pakistan).

Current status: Subjective synonym of *Telescopus rhinopoma* (Blanford, 1874).

***Dendrophis proarchos* Wall, 1910. *J. Bombay nat. Hist. Soc.* 19(4): 827.**

Types: There were 25 syntypes in the type series, from "Sadiya" (one syntype), "North Lakhimpur (Dejoo)" (one syntype), "near Doom Dooma" (one syntype) and "around Dibrugarh" (22 syntypes), all localities being in eastern Assam, north-eastern India. None of the types is known to be extant.

Current status: Subjective synonym of *Dendrelaphis pictus* (Gmelin, 1789).

***Dryophis mycterizans isabellinus* Wall, 1910. *J. Bombay nat. Hist. Soc.* 20(1): 230.**

Type: The holotype was from "Paralai, near Valparai, Anamallay Hills" (= Anaimalai Hills, Tamil Nadu State, south-western India), and cannot be identified at present from a series of unnumbered specimens of *Ahaetulla nasuta* (Lacepède, 1789).

Current status: Subjective synonym of *Ahaetulla nasuta* (Lacepède, 1789).

***Dryophis mycterizans lepidorostralis* Wall, 1910. *J. Bombay nat. Hist. Soc.* 20(1): 229.**

Type(s?): There were one or more syntypes in the original series, from "Bengal" (at the time, included West Bengal State, eastern India as well as Bangladesh, in addition to parts of Bihar State, eastern India), but none can be identified at present from a series of unnumbered specimens of *Ahaetulla nasuta* (Lacepède, 1789).

Current status: Subjective synonym of *Ahaetulla nasuta* (Lacepède, 1789).

***Dryophis mycterizans rhodogaster* Wall, 1908. *J. Bombay nat. Hist. Soc.* 18(4): 919.**

Type: The holotype was from "Shwebo, Upper Burma" (= northern Myanmar), although it cannot be identified at present from a series of unnumbered specimens of *Ahaetulla nasuta* (Lacepède, 1789).

Current status: Subjective synonym of *Ahaetulla nasuta* (Lacepède, 1789).

***Dryophis mycterizans zephrogaster* Wall, 1910. *J. Bombay nat. Hist. Soc.* 20(1): 229.**

Types: The three syntypes were from "Trichinopoly" (= Tiruchirapally, Tamil Nadu State, south-western India), probably "Burma" (= Myanmar), although they cannot be identified from a series of unnumbered specimens of *Ahaetulla nasuta* (Lacepède, 1789).

Current status: Subjective synonym of *Ahaetulla nasuta* (Lacepède, 1789).

***Oligodon evansi* Wall, 1913. *J. Bombay nat. Hist. Soc.* 22(2): 514.**

Type: The holotype was described from "Thandoung, Toundoo District (S. Shan States)" (in north-western Myanmar), and cannot be located in the BNHM collection at present.

Current status: Subjective synonym of *Plagiopholis nuchalis* (Boulenger, 1893).

VIPERIDAE

***Atractaspis wilsoni* Wall, 1908b. *J. Bombay nat. Hist. Soc.* 18(4): 804.**

Type: The holotype was described from "Maidan Mihaftan 30 m. E. of Shushtar in S. W. Persia...between the Zagros mountains and the vast plains of Persian Mesopotamia" (likely to be

Maidan-i-Naftun, now encompassed by the town of Masjed Soleyman, Iran, according to S. C. Anderson, pers. comm., 1998), and cannot be located in the BNHM collection at present.

Current status: Subjective synonym of *Walterinnesia aegyptia* (Lataste, 1887).

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REPRODUCTION IN *GEOCLEMYS HAMILTONII* (TESTUDINES: BATAGURIDAE)

Dhruvajyoti Basu and Suresh Pal Singh

Gharial Rehabilitation Centre, Kukrail, Lucknow 226 015, Uttar Pradesh, India.

ABSTRACT.- The reproduction of the spotted pond turtle, *Geoclemys hamiltonii*, was studied in captivity at Kukrail, Uttar Pradesh. Courtship observed in February and March comprised males mounting and biting the back of the head and neck of females. Nesting was observed in April and May. Five clutches of eggs were obtained; clutch size varying between 13-24. Incubation period was in the range 32-48 days. *G. hamiltonii* exhibits great variation in its nesting season in different parts of its range.

KEY WORDS.- *Geoclemys hamiltonii*, seasonality, incubation, egg dimensions, size at maturity, India.

INTRODUCTION

The spotted pond turtle, *Geoclemys hamiltonii*, is a moderately large batagurid turtle (straight line carapace length to 40.5 cm; Rashid and Swingland, 1997), distributed over the flood plains of the rivers of the northern Indian subcontinent, from the Indian state of Assam in the east to Pakistan in the west (Das, 1995). Information on the biology of this species has begun to accumulate only recently (Rashid and Swingland, 1997; Das, 1991; 1995; Reams, 1997; Bhupathy and Choudhury, 1994; Das and Bhupathy, 1998). This paper presents additional information on its reproduction recorded at the Gharial Rehabilitation Centre, Kukrail, at Lucknow, in northern India, where it has bred in captivity for two consecutive years (1997 and 1998).

MATERIALS AND METHODS

Between September 1987 and August 1994, two males and three females were acquired from waterbodies of adjacent districts of Lucknow and Sitapur in Uttar Pradesh and reared at the Gharial Rehabilitation Centre, Kukrail. Initially, the turtles were reared in concrete pools of dimensions 35.0 x 2.5 x 0.45 m, and subsequently transferred to an exhibition pen in May, 1996. This rectangular pen (dimensions 16.9 x 7.25 m) is fenced with welded metal mesh and approachable for viewing from one short side. The pen encloses two concrete pools of irregular outlines

with water surface areas of ca. 14.8 sq m and 8.6 sq m. These pools are respectively, 0.45 m and 0.75 m deep. Vegetation in the pen includes the trees *Ficus religiosa*, *Dalbergia sisoo*, *Pongamia pinnata* and the shrub, *Tabernomontana coronaria*. The turtles share this pen with 55 other batagurid turtles that occur sympatrically in the wild, of which 33 were of comparable sizes. The turtles spend most of their time in the smaller but deeper pool. There are two small concrete covers in this pen, and *Geoclemys* were occasionally observed spending time under their dark interiors. The turtles were fed once a day with leaves of the mulberry, *Morus alba*, fruits of the fig, *Ficus glomerata*, aquatic plants such as *Hydrilla*, *Potamogeton* and *Ceratophyllum*, and locally obtained freshwater fish.

OBSERVATIONS

Lengths and weights of *Geoclemys hamiltonii* reared in this pen as recorded in 1997 and 1998 are in Table 1. Courtship was observed in the second half of February and in early March. A male was observed mounting the female as she swam about the pool, and to bite the back of the head and neck of the female, sometimes severely enough to produce minor lesions.

Nesting activity was observed on 7 May, 1997 and 26 April, 1998. The entire nesting event on the second occasion is described below:

TABLE 1: Lengths (cm) and weights (kg) of *Geoclemys hamiltonii* from Kukrail.

Date	Sex	Carapace length	Weight
29 June, 1997	Female	30.4	3.84
	Female	28.0	3.00
	Female	24.5	1.75
	Male	26.7	2.25
	Male	27.7	2.75
12 September, 1997	Female	31.7	4.25
	Female	30.0	3.75
	Female	26.8	2.30
	Male	29.7	3.00
	Male	29.3	3.00

The female, carapace length 31.7 cm; weight 4.25 kg, had already begun excavation of the nest hole when first noticed at 1700 hours. She excavated the nest hole 15-20 times with one rear limb over a duration of 0.5-1 min following which she pivoted her body on three limbs to position the other rear limb over the nest hole, which was then used for excavation, before reverting to the first limb once again. The first egg was laid at 1920 hours, and subsequently, eggs were laid at intervals of 1-2 min, to complete laying of 15 eggs by 1937 hours. The female then remained motionless till 1945 hours, and proceeded to cover the nest hole at 1946 hours. Using either hind limb 3-5 times in succession, she completed covering the nest hole by 2006 hours. This female was later identified by cephalic markings and her carapace length and weight on 12.9.98 were 31.7 cm and 4.25 kg, respectively. Nest holes were roughly spherical

and dug near the roots of pen vegetation. The diameter of one such hole was 130 mm.

Eggshells were brittle hardshelled. Eggs were measured with dial vernier callipers and weighed on a counterbalance to the nearest gm. Clutch size, egg dimensions and egg weights for five clutches are presented in Table 2. The third clutch of 1998 was discovered only when the hatchlings emerged from the nest. The other four clutches were incubated indoors in wooden boxes of dimensions 0.75 x 0.60 x 0.45 m in an incubation medium of earth and coarse sand (1:1). Temperature of the medium was recorded once a day with a dial thermometer in 1998. In 1997, the temperature of the medium was maintained in the range 32.5-35° C, but were not recorded daily. Moisture content of the incubation medium was roughly the same as that of medium used for the incubation of *Aspideretes* eggs at the Kukrail Centre, whose value was determined by oven drying to constant weight, to vary from 1.5-4% by weight.

Details on incubation and hatching of *Geoclemys* eggs at Kukrail are in Table 3; the dimensions and weights of hatchlings in Table 4.

DISCUSSIONS

The biology of *Geoclemys hamiltonii* has not been studied in detail, and available information on this species suggests that there might be considerable variation in the timing of reproduction. At present, it is not possible to determine whether this variation is distributional, stochastic or of other origin, but has important implica-

TABLE 2: Data on clutches and eggs of *Geoclemys hamiltonii* at Kukrail. Measurements in mm; weights in gm.

Year	Clutch size	No. of observations	Egg length, range		Egg width range \pm mean		Egg weight range \pm mean	
			Range	Mean \pm SD	Range	Mean \pm SD	Range	Mean \pm SD
1998	15	15	47.6 - 51.2	48.8 \pm 1.2	24.3 - 25.8	24.8 \pm 0.4	15 - 18	17.2 \pm 0.9
	24	24	43.1 - 46.4	44.5 \pm 1.4	24.8 - 27.1	25.8 \pm 0.4	17 - 19	17.7 \pm 0.6
	18	5	41.2 - 48.4	44.4 \pm 3.4	24.8 - 28.2	26.9 \pm 1.3	13 - 17	15.0 \pm 1.6
1997	13	5	43.5 - 44.6	43.8 \pm 0.5	26.1 - 26.2	26.16 \pm 0.05	-	-
	19	4	42.0 - 44.0	43.0 \pm 0.8	25.2 - 26.8	25.9 \pm 0.7	-	-

TABLE 3: Details on incubation and hatching of *Geoclemys hamiltonii* eggs at Kukrail.

Year	Date of nesting	Date of eggs transfer to hatchery	Date of hatching	Clutch size	No. of eggs incubated	No. of hatchlings	% hatching success	Incubation temperature (°C)		Incubation period	Total
								range	mean		
1998	26 April	9 May	22 - 23 June	15	8	18	56.3	29.5 - 32.0	31.9	44 - 45	57 - 58
		9 May	20 - 25 June	24	24					43 - 48	-
		-	30 May	18	-	10	55.6	-	-	-	-
		3 May	3 June	13	11	9	81.8	32.5 - 35.0	-	32	-
1997	7 May	8 May	21 June	19	15	15	86.7	32.5 - 35.0	-	45	45

TABLE 4: Measurements (mm) and weights (gm) of hatchling *Geoclemys hamiltonii* at Kukrail.

Year	Clutch No.	N	Carapace length		Carapace width		Shell height		Shell weight	
			Range	Mean \pm SD	Range	Mean \pm SD	Range	Mean \pm SD	Range	Mean \pm SD
1998	1,2	18	32.6 - 36.9	34.7 \pm 1.4	23.5 - 29.7	27.8 \pm 2.2	17.0 - 20.0	18.3 \pm 0.7	10.0 - 11.0	9.8 \pm 0.8
	3	10	34.6 - 36.7	35.8 \pm 0.8	24.8 - 27.5	26.7 \pm 0.8	18.3 - 21.0	19.7 \pm 0.9	9.0 - 11.0	10.0 \pm 0.7
1997	1	9	35.0 - 37.3	36.3 \pm 0.8	24.2 - 28.2	26.0 \pm 1.1	18.1 - 20.3	19.4	9.4 - 11.0	10.2 \pm 0.6
	2	13	35.5 - 37.3	36.4 \pm 0.5	25.7 - 28.2	27.3 \pm 0.7	19.1 - 20.0	19.6	9.8 - 10.6	10.3 \pm 0.2

tions for the thermal adaptability of the species with regard to embryonic development.

The nesting season of *Geoclemys* in April/May at Kukrail coincides roughly with earlier reports (May in captivity at Florida, USA: Reams, 1997; May and again later: Das, 1995; Das and Bhupathy, 1998; mid-April onwards: Bhupathy and Choudhury, 1994; May, June and July, in captivity in the Netherlands; Rotmans and Rotmans-Zwaal [1994]). These reports are at variance with that of Rashid and Swingland (1997), who, on the basis of the earliest dates females were recorded carrying mature eggs, have stated that nesting by this species in Bangladesh, begins as early as mid-December, and continues till mid-January, followed by a second nesting from late February till early March. Their observations rather concur with those of Das (1991), who, on the basis of local reports, stated October and February to be the nesting season. However, hatching in Bangladesh has been reported by Rashid and Swingland (1997) to coincide with that in Uttar Pradesh, occurring in May/June. If the information from Bangladesh is complete,

then the incubation period of eggs there may range between 55 days (early March to early May) to 180 days (mid-December to mid-June). At Kukrail, incubation lasted 58 days at under 32° C and 45 days at 32-35° C. Reams (1997) has reported an even shorter incubation period of 23 days at 29° C, which is unusual because it is shorter than the incubation period of eggs of any of the 75 species of turtles belonging to nine families reviewed by Ewert (1979). It is also unexpected because it was of shorter duration than that at Kukrail, although occurs at a lower temperature. Rotmans and Rotmans-Zwaal (1994) reported incubation periods of 75-76 days at 30° C. The rather long incubation period of eggs formed in mid-December in Bangladesh can be explained in the light of three reproductive characteristics postulated or observed in chelonians. These are:

- i) retention of eggs after maturation in oviducts;
- ii) embryonic diapause; and
- iii) suspended or extremely slow development at low incubation temperatures.

Ewert and Wilson (1996) have demonstrated that within a species, embryos are capable of expressing diapause depending on the season of oviposition.

Along with *Geoclemys hamiltonii*, *Chitra indica* nests in different seasons in different parts of its range. Rashid and Swingland (1997) have reported nesting between February and May in Bangladesh, while Bhadauria et al. (1990) found the species to nest from end August to mid September in the Chambal River in north-central India, where in fact its nesting begins even earlier, in end-June (unpubl. obs.). Notably, eggs of both *Geoclemys* and *Chitra* incubate rapidly within 40-70 days (Bhadauria et al., 1990; this paper), in comparison with the eggs of several other species of the subcontinent (including *Aspideretes gangeticus*, *A. hurum*, *Lissemys punctata*, *Kachuga tentoria* and *Hardella thurjii*; Basu, unpubl. obsv.), which undergo protracted incubation requiring at least 200 days to hatch. The shift in the nesting season of rapidly incubating species, such as *Geoclemys hamiltonii* and *Chitra indica* in Bangladesh is most likely a response to wetter environmental conditions. Rashid and Swingland (1997) state that at least one third of Bangladesh is inundated every year.

Certain other aspects of the biology of *Geoclemys hamiltonii* have also been further elucidated by the observations at Kukrail and these are briefly described below:

Diet.- *Geoclemys hamiltonii* has been reported to refuse vegetable items of food in captivity by both Das (1995) and Reams (1997). Rashid and Swingland (1997), however, discovered grasses, cereals and plant fibre in stomach contents. At Kukrail too, turtles of this species were observed to devour *Ficus glomerata* fruits and *Morus alba* leaves.

Female size at first reproduction.- The *Geoclemys* at Kukrail, although reared since 1994, did not begin egg-laying until 1997, when the two larger females had attained a carapace length of 27 cm and weight 3.0 kg, as may be seen from Table 1. This size was inferred by Rashid and Swingland (1997) to be the minimum for reproductive maturity in females of this species, which agrees with our own observations, if

the possibility of reproductive immaturity of male *Geoclemys* at Kukrail prior to 1997 is not taken into consideration.

Multiple clutching.- Rashid and Swingland (1997) were in a position to examine the reproductive tracts of females and it may be assumed that they have reported multiple clutching in the species on the basis of definitive evidence, although detailed descriptions of reproductive tracts examined were not presented. Multiple clutching probably occurred at Kukrail in 1998, when three fertile clutches were produced by only two females that were larger than the minimum size at reproduction for females already discussed.

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**A NEW SUBSPECIES OF *PHRYNOCEPHALUS ORNATUS*
BOULENGER (REPTILIA: AGAMIDAE) FROM EASTERN IRAN,
WITH A KEY TO SOUTH-WESTERN AND MIDDLE
ASIAN MICROPHRYNOCEPHALIDS**

Michael Golubev

830 NE Serpentine Pl., Seattle, WA 98155-3619, U.S.A.

Email: mgolubev@uswest.net

(with three text-figures)

ABSTRACT.- A new subspecies of *Phrynocephalus ornatus*, *P. o. vindumi* is described from Iran. It can be distinguished from other south-western and Middle Asian “microphrynocephalids” by having a rose-coloured spot with blue edges on the neck. The species inhabits eastern Iran from Kavir-i-Namak Desert to the Sistan Basin.

KEY WORDS.- *Phrynocephalus ornatus vindumi* ssp. n., Agamidae, Iran, Afghanistan, taxonomy.

INTRODUCTION

Phrynocephalus ornatus, described from Nushki and Helmand, at the borders of Baluchistan, (Pakistan) and Afghanistan (Boulenger, 1887), was first reported from eastern Iran by Nikolsky (1897). Leviton and Anderson (1970), who described the sympatric species, *P. clarkorum* (Anderson and Leviton, 1967), however, noted that Nikolsky’s data needed verification.

Nikolsky (1897) noted important differences in colouration between his specimens and the illustration of the lizard published by Boulenger (1891). The Iranian specimens have two horse-shoe-shaped blue spots divided by a red spot on the neck. He mentioned later that his new specimens’ “variability of pattern consists in a red spot, longitudinally arranged, which divides the blue ones, is broader in some or narrower in other specimens” (Nikolsky, 1900: 393). Anderson (1998) also described this character in his work on the Iranian herpetofauna. According to these data, this spot is rose-coloured with a blue edge in life, whereas one to three pairs of orange or “raspberry” coloured or dark spots may be present on the anterior third of the dorsum in populations from Afghanistan and Pakistan (Smith, 1935; Minton, 1966, Clark, 1992). A single spot of the same colouration may sometimes

be present in the interscapular region (Fig. 1). Boulenger (1891), Clark et al. (1969), and others also do not mention the neck spot in lizards from the eastern part of the range.

Having studied over 100 specimens of these agamas from various parts of the range, including 26 specimens from eastern Iran, I found that colour pattern and other characters of Iranian agamas are stable, for which reason these lizards are being described as a new subspecies of *Phrynocephalus ornatus*.

ABBREVIATIONS USED

CAS- California Academy of Sciences, San Francisco, California, USA

FMNH- Field Museum of Natural History, Chicago, Illinois, USA

MHNG- Museum d’Histoire Naturelle, Geneve, Switzerland

NMBA- Naturhistorisches Museum Basel, Basel, Switzerland

NMW- Naturhistorisches Museum Wien, Wien, Austria

ZIL- Zoological Institute, St. Petersburg, Russia

ZMB- Museum für Naturkunde, Humboldt Universität, Berlin, Germany

ZMMGU- Moscow State University Zoological Museum, Moscow, Russia.

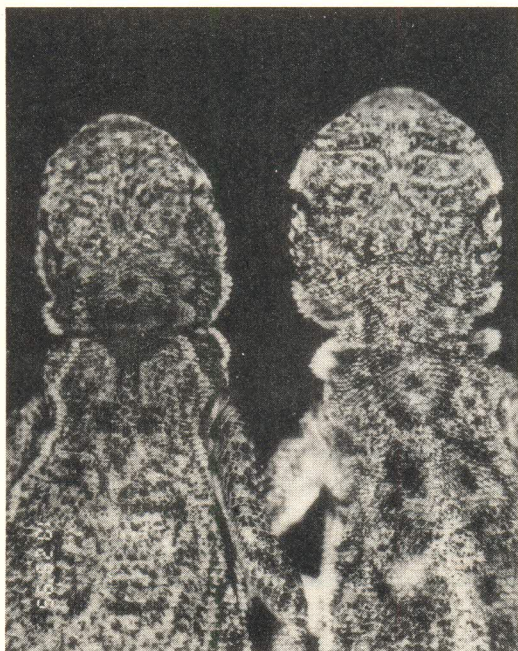


FIGURE 1. 1a: Holotype of *Phrynocephalus ornatus vindumi* (CAS 141204); left; 1b: *Phrynocephalus o. ornatus* (CAS 120204); right.

Phrynocephalus ornatus vindumi

ssp. nov.

(Figs. 1-2)

Holotype (Fig. 1a). CAS 141204. Adult male. Iran: Khorasan Prov.: 35 km. N of Gonabad on road to Torbat-E. Heydariyeh (ca. 34° 49' N, 58° 47' E), 850 m. elevation, S. C. Anderson coll.

Paratypes (Fig. 2). CAS 141204. Adult female. Iran: Khorasan Prov.: 39 km N of Gonabad on road to Torbat-E. Heydariyeh (ca. 34° 41' N, 58° 48' E), October 1975, R. McCullers and S. C. Anderson coll.; MHNG 1591.47. Adult male. Iran: 15 km N Belun (Gonabad), alt. 850 m, 16 April 1974, J. Garzoni and A. de Chambrier coll.; NMBA 4950. Adult male. Chous in terra Zirkuh (Iran); NMW 24796: 1-2. Adult male and female. "Ost Persien" (= eastern Iran); ZIL 8768* two adult males, four adult females, subadult female. Eastern Persia: Zirkuh: after Gyarmakh, 30 June, 1896, N. Zarudny coll. (in Russian); 5207. Four adult males, adult female. E. Persia: Zirkuh Region, khous, 18 April, 1898, N. Zarudny coll.; ZIL 9920. Six adult males. E.

Persia: Neh-i-Bendan Region: Khadji-i-du-chaghi Wall, 2 June, 1901, N. Zarudny coll.; ZIL 9921. Nine juveniles. E. Persia: Zirkuh Region: Bamrud aryk ("aryk" = a type of irrigation canal), 20 June, 1901, N. Zarudny coll.; ZMMGU 2114. Adult male. E. Persia, A. Nikolsky det.; ZMB 15375. Adult female. "Ost Persien" (= eastern Iran), F. Werner coll.

Diagnosis.- V-shaped, horse-shoe shaped or crescentic light spot, rose with blue edges in life, on neck (Fig. 2); small brick-rose dots (faded in alcohol), sometimes edged with dark, scattered spots on dorsum; lower surface of tail tip white in juveniles and adults; snout-vent length (SVL) to tail length (Lcd) ratio of adult males 0.75-0.90, of adult females 0.81-0.89; three to five small subocular shields; no spiny scales along flanks of body, on back of head or thighs; several enlarged scales without spines on front edge of shoulder fold; no light dorso-lateral stripes from eye to tail.

Description of holotype.- Adult male. SVL 34.0 mm.; Lcd 43.5 mm.; SVL/Lcd 0.78; distance between knee-joints (thighs situated at right angle to longitudinal axis of body) 16.1 mm; length of straightened hind limb from tip of fourth toe (without claw) to hip joint 30.4 mm; width of hood 6.3 mm; internostril distance 0.5 mm; 18 scales across midhood (without upper ocular shields); eight scales across hood between rudimentary parietal eye and upper nasal shields; upper nasal shields in contact with each other; lower nasals separated by a scale; four/five small subocular shields which are not differentiated in size from surrounding ones; 99 scales along midbelly from chin to vent; 26 subdigital lamellae under fourth toe.

Head scales keeled, heterogeneous, distinctly enlarged near parietal shield. Keels on scales along dorsum gradually disappear posteriorly; from midback to flanks scales become gradually smaller in size but on flanks they are distinctly

* Six specimens (four catalogued as ZIL 5207 and two as ZIL 8768) are decapitated; the latter series contains a specimen of *Phrynocephalus interscapularis*; all ZIL 9921 specimens are dehydrated and therefore were not studied.

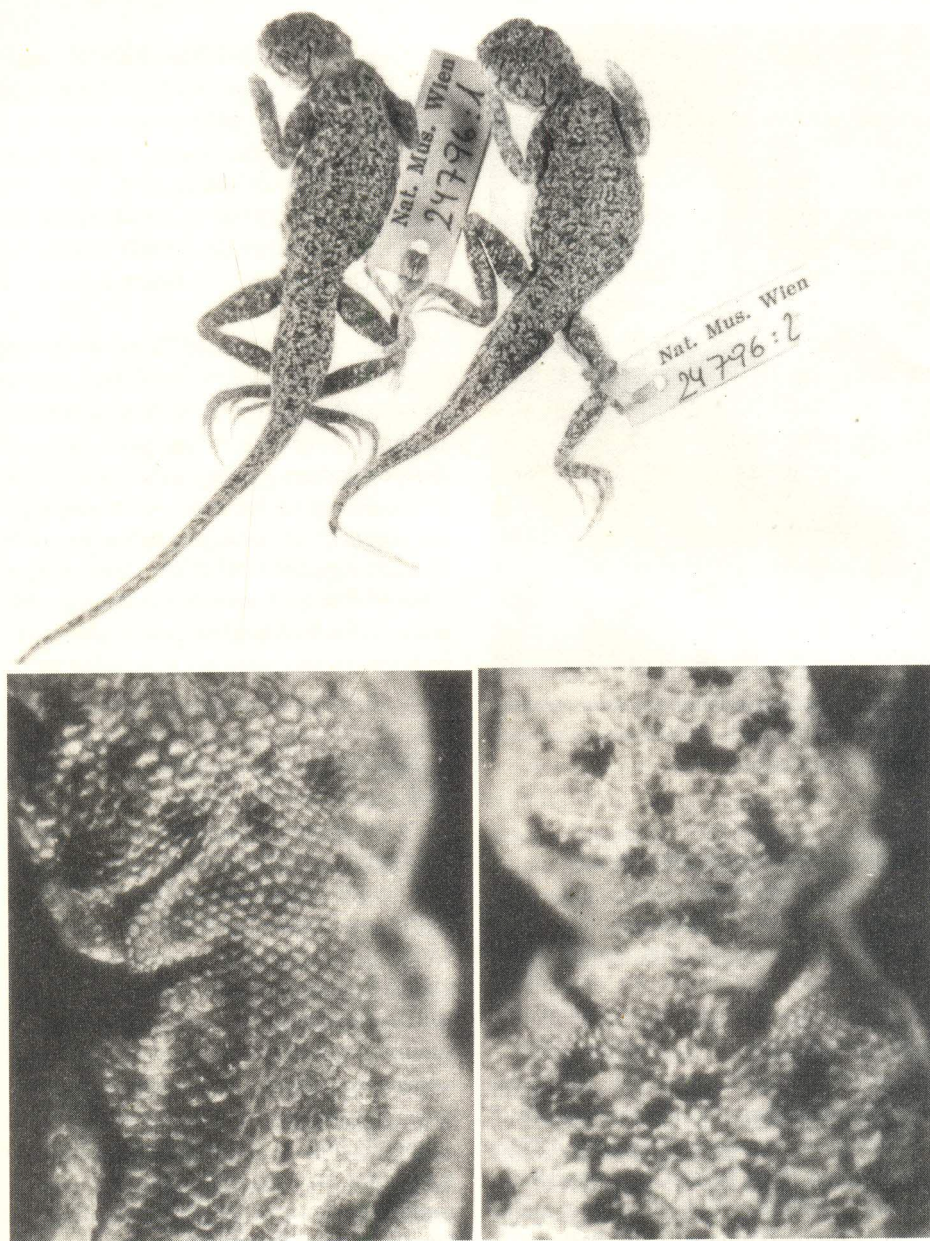


FIGURE 2: The paratypes of *Phrynocephalus ornatus vindumi* (NMW 24796: 1-2): a.-dorsal view (top); b.- and c.- (bottom left and right, respectively); nuchal spot (b- ZIL 5207; c - ZIL 9920).

smaller than other scales. No spiny scales on back of head, on thighs or along flanks; enlarged, smooth scales in front of shoulder fold.

Gular scales large, without keels, granulated. Behind mental are rows of distinct postmental shields, which do not contact lower labials, and end at edge of mouth edge (Fig. 1); one to two

rows of elongated scales, almost equal in size to postmentals, between these rows of chin-shields and lower labials. No distinct keels on abdominal scales.

Caudal scales, both above and below, with distinct keels; upper surfaces of some scales of limbs also with keels. Each subdigital lamella

with single keel which, with other similar keels, form an indistinct row along digit; fringes poorly developed on both sides of fourth toe; claws long and thin.

Colour and pattern of holotype not preserved. In the paratypes (Fig. 2), transverse pattern of light markings (characteristic of a majority of phrynocephalid species) on head; V-shaped, horseshoe-shaped or crescentic light spot on neck; small brick-rose dots (faded in alcohol), sometimes edged with dark, scattered spots on dorsum. Light crescentic spot on neck (covered with skin fold in holotype).

Variation (based on 25 specimens).- SVL (both males and females) 37.5 mm; SVL/Lcd: adult males 0.75-0.90 (0.799 ± 0.019), adult females 0.81-0.89 (0.867 ± 0.049); 18-22 (20.00 ± 0.30) scales across hood (without upper ocular shields); 7-11 (8.61 ± 0.26); scales along hood from parietal eye shield to nasal shields; 90-105 (98.78 ± 0.96) scales along midbelly from mental to vent; 23-31 (26.25 ± 0.38) subdigital lamellae under fourth toe from left side and 23-30 (26.58 ± 0.34) from right side.

Upper nasal shields (n-19) in contact with each other in 94.4%, lower ones- only 33.3%. Orbit of eye (n-19) usually with three to five

small scales (96%) below; the single specimen (NMW 24796:2) has two (from left) and one (from right) enlarged shields (5.4%).

Along each side of body, a light stripe passes through eye, to shoulder fold, above forelimb, and on flanks to base of hindlimb; lower (ventral) part of this stripe between limbs is edged with indistinct dark stripe, and above (dorsal) side, light stripe is edged with indistinct light stripe; the latter becomes more distinct and zig-zag-shaped on sacrum and extends approximately to level of mid-tail; light transverse stripe borders sometimes present at regular intervals between longitudinal stripes after tail base on tail dorsum. There are several black transverse bands on lower surface of tail, but tip is always white in juveniles as well as adults of both sexes.

Distribution.- Besides the localities previously noted for the type series, this lizard has also reported from desert of Zirkuh Region between Villages of Germah (Gyarmah) and Buniabad (Zarudny, 1897), Mudznabad (Mojnabad) and Fenduct, Mudznabad and Bamrud, Bamrud and Magomedabad, Ahangerun and Charakhs, and on the Tag-i-Doroh Plain (Zarudny, 1904). Thus, *Phrynocephalus ornatus vindumi* is distributed in the eastern part of Kavir-i-Namak Desert (E. Iran), along north-eastern slopes of Kelat (Qalat) Range and Kayen Mountains to Iranian-Afghanistan border; it is likely it also occurs in adjoining areas of Afghanistan. The south-eastern part of its range does not extend beyond the Sistan Basin and Farah-Rud River: the allied *P. o. ornatus* inhabits the left bank of this river (CAS 120192-120193 Afghanistan: Juvain).

Habitat.- *Phrynocephalus ornatus vindumi* inhabits "crumbly and soft" sands (Zarudny, 1901, 1904), which is also characteristic of *P. o. ornatus* (Minton, 1966). Nevertheless, the latter is also found "on the bare stony terrain bordering the sand" (Clark et al., 1969: 297).

Comparative notes.- The primary differentiating character of the new subspecies is the colour spot on the back of the head. It is well known that colour spots (the signal spots on the upper surface of the body, spots in the armpits and the colouration of the tail underside) are widely used

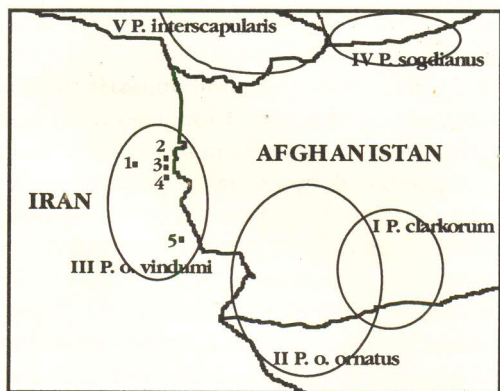


FIGURE 3: Map showing distribution of *Phrynocephalus ornatus vindumi*. Legends are as follows: 1- N of Gonabad on Road to Tarbat-E. Heydariyeh; 15 km. N of Gonabad; 2- Zirkuh Region: Garmah (this locality is plotted from N. Zarudny's, 1896 description of his route); 3- Mozhnabad (W shore of Lake Namakzar); 4- Bamrud; Magomedabad; 5- Neh-i-Bendan Region: Hadji-i-du-chagi.

in the intrageneric systematics of *Phrynocephalus*. Recently it was pointed out that axillary colour spots are not reliable as characters for geographical separation among these lizards (Golubev, 1993a). This indicates that this character, as well as tail ventrum colouration (Golubev, 1993b; unpubl.) is of doubtful value in the systematics of the group. On the contrary, the position of the colour spots on the dorsum is consistent, and when present, is usually of systematic value as indicator of specific differences: *Phrynocephalus boettgeri* and *P. raddei* (scapular region, difference in size), *P. scutellatus* (entire dorsum), *P. helioscopus* (nuchal region), *P. interscapularis* and *P. sogdianus* (scapular region). In *P. o. ornatus*, as was earlier noted, the paired bright raspberry or orange spots are located on the dorsum of body, the unpaired, in the interscapular region (Fig. 1b). In the closely related *P. clarkorum*, these spots are significantly reduced. In two other related species, both found further north in Middle Asia, *P. sogdianus* and *P. interscapularis*, small orange spots are scattered throughout the dorsum (as in *P. o. vindumi*). However, these spots, unlike the nuchal or the scapular spots, are unlikely to be "signal" spots, but are used as camouflage. In one other allied species of "microphrynocephalids", *P. luteoguttatus*, both signal and bright camouflaging spots are absent (Minton, 1966; Clark, 1990). Thus, the nuchal colour spots in the east Iranian populations clearly distinguishes them as a group. It should be mentioned, however, that the presence of such a character of the species level in *P. o. vindumi*, does not necessarily indicate the independence of this species. The absence of spiny fringes on the scales of shoulder folds, along the sides of the body, rear thigh surfaces and head (characteristic of both Middle Asian species), as well as the white tail tip below, pattern of upper surfaces and other characters indicate that *P. o. vindumi* is closely related to the southern *P. ornatus/clarkorum* lineage of phrynocephalids. Despite the range of this form, which occupies an intermediate position between the pairs of northern and southern species (Fig. 3), *P. o. vindumi* seems closer to both Middle Asian microphrynocephalids, if its unpaired

interscapular spot is treated not as camouflage but as an emerging signal spot.

The range of the new subspecies lies entirely within the boundaries of the eastern-north-eastern parts of the so called "East Iranian quadrangle" (Harrison, 1968: 143; 153-156).

Even though a large number of species are found here, *Phrynocephalus ornatus vindumi* is probably the only endemic one. At a first glance this can be easily explained by the openness of this area to penetration of the south-eastern (Afghan-Pakistani), as well as the north-western (Iran-Turanian) elements. At the same time, certain peculiarities of the reptile dispersal in this "corridor" should be noted (the discussion of these is beyond the scope of this article). For example, the complex of most closely related psammophilous forms of "microphrynocephalids" (*P. clarkorum*, *P. ornatus*, *P. sogdianus*, *P. interscapularis*), macrophrynocephalids" (*P. euptilopus*, *P. mystaceus*), lacertids (*Eremias fasciata*, *E. lineolata*, *E. scripta*) or gekkonids (*Crossobamon orientalis*, *C. eversmanni lumsdenii*, *C. e. eversmanni*), which apparently have dispersed from the south-east to the north, have formed a semi-circle around the area of the Paropamisus and Hindukush Mountains, penetrating further into Turan (Golubev, 1995), but are absent from the sand massifs of the Dasht-i-Kavir and Dast-i-Lut Deserts. These facts suggest the existence of recent obstacles to the dispersal of the plain psammophilous reptiles and a complex developmental history of these territories. Stöcklin (1968: 1256) considers this region to be "much more closely related to the Baluchistan-Indus Ranges" than to the Iranian Plateau. The geomorphologic evolution of Iran and Afghan-Pakistan plains, the changes in their landscapes and climate, have not been studied in sufficient detail. Recently, evidence of glacial moraines was found in the territory of Iran (Kerman; Djebalbarez), and no fewer than three pluvial periods of the Pleistocene were noted (Selivanov, 1980; 1982; 1983). On the Iranian uplands, the length of the Quaternary glaciers would have reached 15 km, the periglacial relief

on their periphery was distributed at the elevations of 3,800-1,800 m, whereas at present, small glaciers remain on Elbrus Mountain (Ananyev and Leontyev, 1987). Three to four stages of change in the climate conditions in the Pleistocene is indicated for Sistan and Baluchistan (Sarvati, 1993). Earlier, Sarvati (1986) mentioned that the Kevire Nemek Depression experienced tectonic settling throughout the Pleistocene. The events of that time were, in all probability, determined the shaping of the region's herpetofauna (Anderson, 1968; Leviton and Anderson, 1984).

Etymology.- The author takes pleasure in naming this new form for Jens V. Vindum, Collections Manager, Department of Herpetology, California Academy of Sciences, San Francisco.

Key to SW and Middle Asian forms of microphrynocephalids.-

1a. SVL/tail ratio > 0.93 (0.93-1.07; mean 0.99) in adult males, 1.03 (1.03-1.16; mean 1.09) in adult females; dorsum reticulated

..... *P. luteoguttatus* Boulenger

1b. SVL/tail ratio < 0.96 in adult males, adult 1.04 in females 2

2a. Spiny scales along flanks, back of head, thighs and front of shoulder folds; lower surface of tail tip black 3

2b. No spiny scales along flanks, on back of head, thighs and on front of axillary folds; lower surface of tail tip white 4

3a. Signal spot on scapular region always present; one or two (rarely, three) enlarged subocular scales; pattern of dorsum includes small dark and light dots

..... *P. interscapularis* Lichtenstein

3b. Signal spot on scapular region sometimes absent; four or five (rarely, three) enlarged subocular scales; pattern of dorsum includes dark-brown dots

..... *P. sogdianus* Chernov

4a. Light dorsolateral stripes from eye to tail; one or two enlarged subocular scales

..... *P. clarkorum* Anderson & Leviton

4b. No dorsolateral stripes from eye to tail; three to five subocular scales 5

5a. Several paired orange or raspberry coloured spots along dorsum, unpaired spot of same

colour may be presented on shoulders; SVL/tail ratio 0.71-0.78 (0.75) in adult males, 0.73-0.82 (0.78) in females

..... *P. o. ornatus* Boulenger

5b. Single rose with blue edged spot on neck; SVL/tail ratio 0.75-0.90 (0.80) in adult males, 0.81-0.89 (0.87) in adult females

..... *P. o. vindumi* ssp. n.

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CONSERVATION ASSESSMENT OF THE HERPETOFAUNA OF INDIA- AN OVERVIEW

Sanjay Molur¹ and Sally Walker²

Zoo Outreach Organisation/ CBSG India
79 Bharathi Colony, Peelamedu, Coimbatore 641 004, India

¹Email: herpinvert@vsnl.com

²Email: zooreach@vsnl.com
(with one text-figure)

ABSTRACT.- In 1997, a series of Conservation Assessment and Management Plan (CAMP) workshops were conducted to assess the status of selected groups of flora and fauna in India. The CAMP process methodology, developed by the Conservation Breeding Specialist Group of the IUCN/SSC, is participatory, objective, technical and systematic in approach to assess the status of every species. The basis for the assessment is the IUCN Red List categories. A total of 652 taxa were assessed at the workshops for amphibians and reptiles, 202 amphibians and 450 reptiles, and information on distribution and threats to the taxa compiled, the current knowledge regarding species and extent of information, or lack of it, available with respect to species identified, recommendations for future research and future management to improve species prospects made, and an understanding of a species scenario for compiling an action plan for survival of the species gained.

KEY WORDS.- Conservation Assessment and Management Plan, IUCN Red List, amphibians, reptiles, conservation, India.

INTRODUCTION

In 1997, eight Conservation Assessment and Management Plan (CAMP) workshops were conducted under the auspices of different organizations. These focused on selected medicinal plants of southern India, selected medicinal plants of northern, central and north-eastern India, selected soil invertebrates of southern India, amphibians of India, reptiles of India, mangroves and related flora and fauna of India, mammals of India and selected freshwater fishes of India. Six of the eight workshops were conducted under the Biodiversity Conservation Prioritisation Project for India organised by World Wide Fund for Nature, World Resources Institute and The Nature Conservancy, sponsored by USAID. The Zoo Outreach Organisation/Conservation Breeding Specialist Group India coordinated and facilitated the workshops.

The amphibian and reptile workshops were conducted from 22-26 April, 1997 and 19-23 May, 1997, respectively, with 29 participants

from 25 institutes for the former and 36 participants from 23 institutes for the latter. In total, 652 taxa were assessed at the two workshops, comprising 202 amphibians and 450 reptiles.

METHODOLOGY

The CAMP workshop process employs the IUCN categories as a tool in assessing species status in a group (see details of the CAMP process in Ellis and Seal, 1997). The IUCN categories were revised in 1994 and ratified by the IUCN for use in threat categorisation at the global level (IUCN, 1996). The structure of the categories includes extinct, threatened, non-threatened, data deficient and not evaluated divisions; the first three divisions are further split into subcategories. The structure of the IUCN Red List categories is given in the figure below. Since 1991, the old Red Data Book categories have undergone successive changes to accommodate general guidelines for across taxonomic groups. The 1991 version of the Red List category

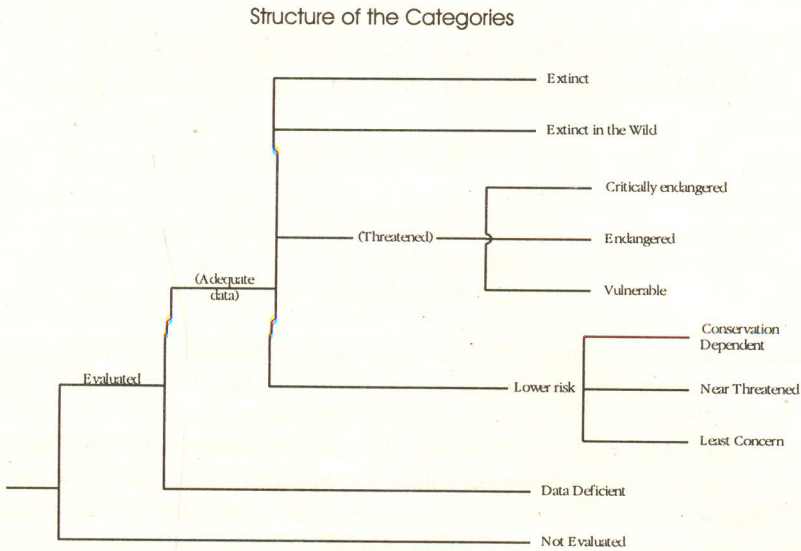


FIGURE 1: Structure of the threatened categories. See IUCN (1996) for details.

ries was applicable only to large mammals/vertebrates, while further revisions included fine tuning of the categories to fit other taxonomic groups of both plants and animals, except micro-organisms. Simultaneously, the revisions also introduced the non-threatened categories, which have been defined in the 1994 version. To make application of the categories more universal, numerical values were attached to the different criteria for threat categories and the final version also includes a purely quantitative criterion which involves computation of the probability of extinction (such as in a population viability analysis) over a time frame for a taxon. The 1994 version of the Red List threatened categories are derived through a set of five criteria based on which the threatened category is assigned. The term "threatened" according to the 1994 IUCN categories includes: Critically Endangered, Endangered or Vulnerable. The five criteria for threat categories (IUCN, 1994; Mace and Stuart, 1994) are:

- a) Population Reduction
- b) Restricted Distribution
- c) Population Restriction and Extreme Fluctuation
- d) Restricted Population
- e) Probability of Extinction

For a taxon to be categorized as Threatened, it needs to qualify for any one of the above five criteria only. Not qualifying for the above criteria could mean that a taxon is either not threatened or data is deficient to arrive at a conclusion.

The IUCN categories are best applicable only at the global level. Regional or national application cannot be fairly carried out in the present context unless the taxon to be assessed is endemic to the country or the region, or, the taxon exists as an isolated population in the country with no migration of individuals or gametes between other conspecific populations (Gärdenfors, 1996). However, the current version of the IUCN categories is being employed to assess the national status of taxa for want of suitable guidelines for localized assessments. In the Indian CAMP workshops, all Indian endemic amphibians and reptiles were assessed first, followed by assessment of non-endemic taxa at the national level. The categories and the criteria used to derive the threat categories are indicated for the level of assessment of a taxon as either global or national assessment.

Assessments at the workshops have been made from information gathered from participating biologists, from their knowledge in the field, including unpublished information of range extensions, sightings, local threats, habitat

TABLE 1: Data quality of the herpetofauna assessed at the CAMP workshop.

Data quality	Amphibians		Reptiles	
	Endemics	Non-endemics	Endemics	Non-endemics
Census and monitoring	3	0	3	11
General field studies	93	58	123	108
Informal field studies	7	0	31	76
Indirect information	0	0	0	23
Records, museum, literature	38	22	103	170
Hearsay, popular belief	0	0	0	1

changes, impact of changing ecology and other important information that does not normally get published. Literature sources are also sought in compiling this information, and museum records, if available, are included. After the initial compilation of data in a Taxon Data Sheet, the status is derived using qualifiers (or criteria) for the degrees of threat and the information is ratified at an open plenary in the workshop. The information in the Taxon Data Sheet is then compiled and a draft sent to all participants for review.

DATA QUALITY

Information provided at the workshop is in different grades of scientific scrutiny. The types of data used in assessing a taxon can be

- a) Census and monitoring studies
- b) General field studies
- c) Informal field sightings
- d) Indirect information such as from trade, etc.
- e) Records, literature, museum, collections, etc.
- f) Popular belief or hearsay.

Information obtained at the workshop varied tremendously depending on the taxa that was being assessed. A few taxa with many studies such as some ranids, crocodiles, some turtles and some snakes were evaluated with current information on their populations and habitat. Most of the others were assessed based on past records and information from general field studies. The assessment also included some taxa (such as those described by the Indian herpetologist, C.R.N. Rao), for which no information on habi-

tat or population is available. In fact, many of the type specimens are lost and the taxa are in need of revalidation (Dutta, 1997b). Such taxa were assessed as Data Deficient. All species belonging to the family Hydrophiidae were assessed as Data Deficient since nothing is known about this group.

The IUCN Red List categories recognises the fact that detailed population and habitat information are rarely available and in such instances, inferences must be used to the extent possible without compromising on the validity of such judgements (IUCN, 1994). Factors such as the effects of threats, catastrophes, human action, pathogens and invading species need to be considered equally seriously in evaluating the status. Mere dependence on scientific data and further validation will mean that every taxa will be classified as Data Deficient, however well studied it may be. Table 1 indicates the number of taxa assessed according to the above kinds of data quality.

RESULTS

Endemism.- The south Asian region has a rich diversity of amphibians and reptiles, of 878 species (Das, 1994). India has a high representation of endemic amphibians and reptiles, especially in the Western Ghats. A few are also endemics to the north-eastern Indian states, but many more are not because of the jagged Indian political boundary that bisects the eastern Himalayas (a known hotspot of biological diversity) and the neighbouring faunistically similar regions of south-eastern China and northern Myanmar. In-

TABLE 2: Areas of amphibian and reptile endemism within India.

Area	Amphibians	Reptiles
Western Ghats	93	98
Andaman and Nicobar Islands	6	27
Eastern Ghats	0	9
Southern India (incl. Western Ghats)	2	11
North-eastern India	22	15
Northern India	3	13
Other parts of India	3	24
Total	129	197

dia, in general, has a high representation of political endemics- 63% amphibians and 44% reptiles (Table 2). The Western Ghats are home to some unique endemics; amphibian genera: *Gegenophis*, *Indirana*, *Indotyphlus*, *Melanobatrachus*, *Micrixalus* sensu stricto, *Nyctibatrachus* and *Uraeotyphlus* are unique to this area. Among reptiles, the genera *Brachyophidium*, *Melanophidium*, *Plectrurus*, *Ristella*, *Teretrurus* and *Xylophis* are unique to this region. Western Ghats has 93 amphibian taxa and 98 reptilian taxa endemic (Molur and Walker, 1998a; 1998b); the proportion of endemics in the Western Ghats to the rest of the country is as high as 72% and 50%, respectively. Checklists of Indian reptiles and amphibians have been published over the years (Inger and Dutta, 1986; Dutta, 1992; Das, 1994; 1997; Das and Dutta, 1998). Inger and Dutta (1986) listed 181 species of amphibians in India. Dutta (1992) revised the earlier list to include 197 species and made some major revisions in the taxonomy at both generic and specific levels. Dutta (1997b) subsequently published the book, "Checklist of amphibians of India and Sri Lanka", which listed 216 taxa of Indian amphibians. However, based on a list provided by Indraneil Das, the participants at the amphibian CAMP workshop drew up a list of 205 taxa (Molur and Walker, 1998a). Between then and the recent list of Indian amphibians by Das and Dutta (1998), seven more species have been described (Das, 1997; 1998a; 1998b; Das and Chanda, 1997; Das and Ravichandran, 1997; Dutta, 1997a; Ravichandran, 1997) increasing the total am-

phibian taxa in India to 212. Das (1994) prepared a similar list for the reptile taxa of south Asia and a more recent list of reptiles of India (1997) which has 484 species. Inclusive of subspecies, the total reptilian taxa according to this checklist is 508. Das's checklist was the basis for assessment at the workshop, which due to constraints of time could not assess all known taxa. However, there were a few species not included in Das's checklist, that were assessed at the workshop- *Mabuya multicarinata*, *Trimeresurus albolabris septentrionalis* and *Eryx johnii persicus*. These taxa have not been included in the Indian checklist by Das as they are not known from the political boundaries of Republic of India.

Status of amphibians and reptiles in India.- The CAMP workshops for the first time assessed all of the amphibians of the country and nearly 85% of the reptiles of the country. This is the first instance of a country carrying out such an exercise anywhere in the world although CAMP workshops have been held in over 30 countries. These activities were in keeping with the recommendations by the Convention on Biological Diversity. Assessments were made at the global and national levels for endemics and non-endemics respectively. A sizeable proportion of herpetofauna in India are threatened with extinction in either immediate, near or medium-term future.

Ninety-eight taxa of amphibians (48%) and 198 taxa of reptiles (40%) are threatened in India (Table 3). The proportion of endemic taxa threatened is a staggering 59% and 56% respectively for amphibians and reptiles. The principle reason for the endemic taxa to be threatened is because of their highly restricted distribution. More than 78% of endemic amphibians and reptiles were assessed as threatened because of their restricted distribution (total distribution range not exceeding 20,000 sq. km, Extent of Occurrence and/ or 2,000 sq. km, Area of Occupancy). A high proportion of the remaining threatened taxa were assessed as such because of restricted population (found in less than five locations). Only two amphibians and three reptiles were assigned to threatened categories due to population declines.

TABLE 3: Status of amphibian and reptile taxa in India.

Status	Amphibians		Reptiles	
	Endemics	Non-endemics	Endemics	Non-endemics
Extinct (EX)	0	0	0	0
Extinct in the wild (EW)	0	0	0	0
Critically endangered (CR)	10	0	16	16
Endangered (EN)	24	18	32	20
Vulnerable (VU)	42	4	62	52
Lower risk - Near threatened (LRnt)	21	36	37	68
Lower risk - Least concern (LRlc)	2	6	9	38
Data Deficient	28	11	41	59
Total evaluated	127	75	197	253
Not Evaluated	2	1	0	50+

TABLE 4: Criteria of threat to the herpetofauna of India.

Criteria of threat	Amphibians		Reptiles	
	Endemic	Non-endemic	Endemic	Non-endemic
Population Reduction	3	4	3	16
Restricted Distribution	70	17	79	62
Population Restriction and Extreme Fluctuation	0	0	0	3
Restricted Population	16	0	47	20
Probability of Extinction	0	0	0	0

A higher ratio of threatened endemic taxa due to restricted distribution is reflected in the fact that 22 amphibians are recorded from less than 10 locations, 43 taxa are recorded from less than five locations and 47 taxa in a single location. Similarly, 23 taxa of reptiles are recorded from less than 10 locations, 86 taxa from less than five locations and 56 taxa from a single location.

Of the non-endemic taxa in India, restricted distribution once again is a major factor (78% of non-endemic amphibians and 61% of non-endemic reptiles) for their threat status. However, the reason for this is widespread distribution of many species found in northern, north-western and north-eastern parts of India which spillover political boundaries. These taxa have a restricted distribution within India, whose inclusion for assessment is for political area alone. According to the IUCN, application of the 1994 categories at the national or regional level is not ideal, but also not totally incorrect for a national assessment, keeping in mind the country's

management needs. However, isolated population in the country with no gametic or individual exchange between other populations outside can be assessed confidently using the IUCN categories (Gärdenfors, 1996). Certain taxa found in the Andaman and Nicobar islands are obviously isolated from the mainland population in south-east Asia; some taxa found in the Western Ghats are similarly isolated from their conspecifics in Sri Lanka.

Combined with a highly restricted distribution, multifaceted threats are afflicting many herpetofaunal populations in the country. Both amphibians and reptiles are threatened due to loss of habitat, habitat fragmentation and human interference in various forms. In case of reptiles, specific threats include hunting for local use (food and medicine) and trade. Fishing is an indirect threat affecting some reptiles such as freshwater and marine turtles and *Gavialis gangeticus*. Threats such as the above are fairly well documented or inferred from studies in the

field, like drying up of streams, changes in vegetation, cattle grazing, clearing of habitat for human developmental projects, loss of habitat due to damming, among many other obvious threats. However, there are other reasons that have been indicated as forcing these groups into extinction, such as pollution, pesticides, changes in edaphic factors, decline in prey species, which are suspected to be threats but have not been validated scientifically.

Status of amphibian and reptile field studies in India.- The assessments at the CAMP workshops were conducted as a first step to understand the status of amphibians and reptiles in India. However, the workshops also revealed many lacunae and anomalies which prevent complete understanding of the status of amphibian and reptile taxa in the wild:

Taxonomic problems.- Taxonomic confusion abounds in the herpetofaunal lists of India. The reasons for this were investigated at the amphibian CAMP. A number of taxonomic rearrangements in amphibians have been suggested since 1985 by the French herpetologist, Alain Dubois, a system that few field biologists in India are familiar with. Dubois established or revived old genera and species and synonymised subspecies and species for the past 23 years (Dubois, 1975; 1983a; 1983b; 1985; 1986a; 1986b; 1987a; 1987b; 1992). Dutta (1992; 1997a; 1997b) has, in general, followed this nomenclature. Other researchers have worked on amphibian systematics (e.g., Chanda and Sarkar, 1997; Chanda and Das, 1997), adding, deleting or modifying the faunal lists. Dutta (1997b) in the introduction to his book "Amphibians of India and Sri Lanka" has mentioned the works produced in the 19th century and early 20th century, starting from Günther (1864) who produced the monograph to the reptiles (and amphibians) of British India. The scenario for reptiles is no different compared to amphibians. A look at the recent issues of the Indian herpetological journal, *Hamadryad*, shows a growing number of papers dedicated to changes in reptile systematics (David and Vogel, 1998; Das, 1994; 1997; Wüster, 1998a; 1998b). Das (1992), in an overview on additions and taxonomic changes in the

herpetofaunal lists in south Asia, has compiled developments in the field after 1987 where he lists numerous changes in herpetofaunal systematics. Many taxa are at present being revised, such as the *Ophiophagus hannah*, and the *Limnonectes limnocharis* species complexes and the validity of certain other ranids. All of the above examples indicate the complexity of amphibian and reptile taxonomy in south Asia, which will remain one of the major stumbling blocks in understanding, studying and assessing the herpetofauna of India. Further, different schools of thoughts lend their share of complexities.

A specific example of the state of amphibian taxonomy is illustrated by the microhylid, *Microhyla ornata*. Chromosomal counts of this species in labs in India and China reveal differences between the populations from India and China (Prakash, 1998). Cytogenetic (karyotyping) and molecular genetic studies are important tools for verification of taxonomic validity among amphibians and reptiles. Some of the common complaints in taxonomic confusions in India include:

- a) non-availability of literature, especially papers that are printed in foreign languages or abroad,
- b) lack of identification resources (the most commonly used guides to amphibians being Boulenger (1890; 1920),
- c) scarcity of systematic collections for verification of specimens (in some cases the type specimens are either badly preserved or lost)
- d) a general misunderstanding between field biologists and taxonomists regarding taxonomy, systematics and distribution ranges due to the above problems and lack of communication.

Inconsistent field techniques.- It was observed at the workshop that different field biologists had followed different methodologies in surveys, density counts and population studies. In many cases, much of the information provided gave an overall picture of the population but not comparable between regions. Further, most studies were not conducted from a monitoring

and population point of view, rather they were basic surveys and field observations including casual forays into the forest for collections.

Studies of herpetofauna in the field and the impact of changing ecological factors is in its infancy stage. Natural history observation and collection driven studies have dominated this field in India, whereby, the interpretation of these studies and the habitat features observed make it difficult to interpret the interacting factors from the viewpoint of conservation biology. Population ecology is yet to be recognised as an important aspect of conservation biology of amphibians and reptiles. One of the common feelings at the workshops was that some amphibians and reptiles are so "abundantly" found that these populations cannot be considered as small even with obvious threats such as loss of habitat. Large numbers obviously still play a big role in the minds of field biologists, rather than a hard look at the dynamics within the population structure over the years. Most of the studies in the recent past has been of range extensions and new records and none on population size or structure.

Lack of knowledge of threats to herpetofauna.- Threats as indicated in the workshops are more obvious and all pervading due to man's actions. More subtle threats such as pollution, fungal and viral infection and ultraviolet radiation, are yet to be studied in India. Amphibian declines around the world are being ascribed to either or all of the above reasons, though in India or the neighbouring countries, such studies are yet to begin. A few studies on status and threats to reptiles have been conducted, but again in only a few species and restricted to small areas (e.g., Andrews and Whitaker, 1994).

Charisma and the herpetofauna.- Why have amphibians and some reptiles been so neglected compared to large mammals or birds? Are amphibians and reptiles too small, slimy or ugly to attract the same amount of scientific interest as mammals? Perhaps large mammals are more visible, a fact that is substantiated by the fact that some interest in large reptiles such as crocodiles and sea turtles did develop along with the larger mammals. Studies on amphibians, small reptiles and invertebrates were restricted solely to their

descriptions by various British, French, Dutch and German naturalists up to the mid-20th century. A few early Indian researchers also followed in the footsteps of the foreign naturalists after independence. It is only recently that a fresh crop of researchers is delving into the vast, "less attractive" area of amphibian and reptile studies, not only with respect to new descriptions but also distribution studies and effects of man's influence on their habitat. If this is any indication to go by, scientific studies on the herpetofauna in India has just had its second birth!

Taxonomists, an endangered species.- Unfortunately, the study of systematics and taxonomy in India are on the wane. Only a handful of taxonomists exist today to identify, describe or revisit taxonomic confusion among amphibians and reptiles. With all the difficulties field biologists face at present in identifying the components of the herpetofauna, scarcity of taxonomists is another threat that future researchers may face. Indian biodiversity is still so vastly unexplored, that there are still many mammal (e.g., rodent and bat) species that are undescribed (M. Muni, pers. comm., 1997; G. Marimuthu, pers. comm., 1997; M.S. Pradhan, pers. comm., 1997; I. Prakash, pers. comm. 1998; I. Das, pers. comm., 1998) leave alone the many amphibians and reptiles and the innumerable invertebrates! A quick look at the recent issues of *Hamadryad* shows at least six new species of amphibians described in the last two years, and many more unworked material are at hand, the formal descriptions of which may take several years (I. Das, pers. comm., 1998). Table 5 shows the growth of the herpetological fauna over time.

Patchy surveys.- Many endemics have been recorded from single locations; a point that many researchers feel may be due to the highly restricted nature of certain taxa. This however, may not be universally true since many range extensions have been recorded continuously and, in some cases, sightings of frogs after a fifty to hundred years have been made (as in the case of *Melanobatrachus indicus*; see Daltry and Martin, 1997; Roux, 1928; Vasudevan, 1997). Inconsistent methods in surveys and field techniques have lead to patchy recording of many taxa

CONCLUSIONS

The CAMP workshops on amphibians and reptiles have helped in understanding the status of not only individual taxa in the country but also the various problems plaguing the conservation of these taxa. The state of field research and the complementary lab research are at an infant stage, which need to be synchronised and intensified in the years to come. Regular field surveys and monitoring projects alone can determine the population dynamics of these taxa, which may otherwise seem "abundant and safe". Periodic studies will also help resolve suspected declines or absence of a taxon due to "lack of sighting" in a particular season. Amphibian and reptile distribution of many endemics is still quite patchy, again because of a lack of periodic monitoring.

The CAMP results indicate an overall status of the taxa and do not go into the details of how individual threats are impacting taxa. That information, however, is lacking in the current methodologies used in studying herpetofauna. Threats other than the obvious loss of habitat and human interference have not been documented in detail, an important drawback that may prove costly in the future if any of the non-obvious threats such as ultraviolet radiation or viral infections take their toll. For organisms such as amphibians that are considered as biological indicators, influences of pollution and pesticides need to be studied intensively, and not be end as a Master's dissertation work in a University laboratory.

Changes in names of species, which is responsible for much confusion among local biologists, need to be tackled at a more open level, involving many more biologists and related field and laboratory researchers. Identification keys and manual need to be developed for distribution among field biologists, and local museums and preserved specimen holding facilities need to reorient their curation procedures to make these more accessible to field workers. A standard field manual specific for the country on the lines of the book by Heyer et al. (1994) is required.

The recommendations of the CAMP workshops in some ways provide a focus to biologists in future data collection and fieldwork, apart from

actually identifying lacunae areas of research. The results of the first CAMPs are akin to "first information report" and they need to be followed up in the next three to five years to understand future priorities. The authors warn, however, that the CAMP process should not be used as a justification to end specimen collections and thereby, systematic research. Taxonomic clarity is essential to the process of inventories, population studies, conservation action plans, and finally, management plans for conservation.

Based on past studies and the trends in populations of amphibians and reptiles in India, recommendations were made by the workshop participants. Due to the above difficulties and lacunae in research, the participants suggested that survey and monitoring be carried out periodically. Habitat management was also recognised as an important management recommendation since many threats involved habitat and changes in the same. Taxonomic and genetic studies were recommended as an immediate need to resolve some difficult questions in systematics. Other recommendations include limiting factor research, that are not obvious but suspected to play a role in the population dynamics of a taxon. Population and Habitat Viability Assessment (PHVA) was recommended for many amphibians and reptiles because of the threats acting on them and their decline in the wild. A PHVA would help in understanding probabilities of extinction for a given taxon, provided enough biological information is available.

Captive breeding was recommended for 94 threatened amphibians and reptiles of India. Amphibians and the smaller reptiles are relatively easy to keep and breed in captivity compared to larger reptiles (such as crocodiles) and mammals. Human resources and financial requirements are also relatively modest for the smaller herpetofauna. Further, captive breeding for conservation can, in general, be implemented successfully with the smaller herpetofauna since their reintroduction into the wild does not carry with it the negative impact on humans in the area that a crocodile or a large mammalian carnivore might attract.

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A CHECKLIST OF CHROMOSOME NUMBERS OF SOUTH ASIAN REPTILES

Indraneil Das¹ and Hidetoshi Ota²

¹Institute of Biodiversity and Environmental Conservation, Universiti Malaysia Sarawak,
94300, Kota Samarahan, Sarawak, Malaysia

Email: idas@mailhost.unimas.my

²Tropical Biosphere Research Center, University of the Ryukyus,
1 Senbaru, Nishihara-cho, Okinawa 903-01, Japan.

Email: ota@sci.u-ryukyu.ac.jp

ABSTRACT.- The chromosome numbers of 119 species of reptiles that occur in the south Asian region are listed. The inventory includes three crocodiles, 13 turtles, 54 lizards and 49 snakes. This represents about a fourth of the known species of the subcontinent. Cytogenetic information in many cases offers clues to the detection of cryptic species overlooked by morphological taxonomists.

KEY WORDS.- Chromosome numbers, karyotype, reptiles, taxonomy, south Asia.

INTRODUCTION

The chromosome numbers of 119 species of reptiles known to occur in southern Asia, are presented. The inventory includes three crocodiles, 13 turtles, 54 lizards and 49 snakes. Several of these derive from studies conducted on extralimital populations. In some of these and other cases, genetic differences provide clues to the existence of biological and evolutionary cryptic species that have been overlooked by morphological taxonomy. Examples of widespread nominal species with possible karyological variation include: *Bronchocela cristatella*, whose diploid number (2n) has been given as 48 by Moody (1980) in Olmo (1986; see below) and 34 by Solleder and Schmid (1988) and *Xenochrophis piscator*, whose 2n karyotypic count is 40, and 42, according to Sharma and Nakhasi (1980) as well as 42 according to DeSmet (1978).

In many such instances, because the provenance of the specimen karyologically investigated was not mentioned, it is unclear whether these reflect karyotypic differentiation among different populations, or actually show chromosome polymorphism within single populations.

In summary, about three-fourths of the reptile species occurring in the Indian region lack karyological data. The situation is similar to that

of the region's amphibian fauna, for which 85 per cent of taxa lack similar genetic database (Prakash, 1997).

CROCODYLIA CROCODYLIDAE

Crocodylus palustris Lesson, 1831:

Karyotype: 2n = 30 (Cohen and Gans, 1970; Prakash and Sinha, 1995; Singh et al., 1968: from India).

Remarks: Analyses of mitochondrial and ribosomal DNA of *Crocodylus kimbula* by Densmore and White (1991) support the argument for a specific status for the Sri Lankan population, which is occasionally regarded as a subspecies of *C. palustris*.

Crocodylus porosus Schneider, 1801:

Karyotype: 2n = 34 (Chavananikul et al., 1994: from Thailand; Cohen and Gans, 1970; Gorman, 1973).

GAVIALIIDAE

Gavialis gangeticus (Gmelin, 1789):

Karyotype: 2n = 32 (Cohen and Gans, 1970; Prakash and Sinha, 1995; Singh et al., 1968: from India).

TESTUDINES
DERMOCHELYIDAE

***Dermochelys coriacea* (Vandelli, 1761):**

Karyotype: $2n = 56$ (Medrano et al., 1987; French Guiana).

CHELONIIDAE

***Caretta caretta* (Linnaeus, 1758):**

Karyotype: $2n = 52$ (male) and $2n = 51$ (female) (Nakamura, 1937: from Japan); $2n = 58$ (male) and $2n = 57$ (female) (Nakamura, 1949: from Japan); $2n = 58$ (Gorman, 1973); $2n = 56$ (Bickham, 1981; Kamezaki, 1989: from Japan).

Remarks: See Remarks under *Lepidochelys olivacea*.

***Chelonia mydas* (Linnaeus, 1758):**

Karyotype: $2n = 56$ (Bachmere, 1981: from western Indian Ocean; Bickham et al., 1980: from Venezuela, Philippines, Nicaragua and Surinam); $2n = 56$ (male) and $2n = 55$ (female) (Makino, 1952: from Japan).

***Eretmochelys imbricata* (Linnaeus, 1766):**

Karyotype: $2n = 56$ (Bickham, 1981; Kamezaki, 1990).

***Lepidochelys olivacea* (Eschscholtz, 1829):**

Karyotype: $2n = 56$ (Bhunya and Mohanty-Hejmadi, 1986: from eastern India).

Remarks: The $2n = 52$ (male) and $2n = 51$ (female) karyotypes of Nakamura (1937) and $2n = 58$ (male) and $2n = 57$ (female) karyotypes of Nakamura (1949), both reported as of *olivacea*, were actually based on *Caretta caretta*. (See Nishimura and Hara [1967] for a review of taxonomic confusions involving the two species in Japan.)

BATAGURIDAE

***Cuora amboinensis* (Daudin, 1801 "1802"):**

Karyotype: $2n = 52$ (Carr and Bickham, 1986; Killebrew, 1977; Stock, 1972); $2n = 50$ (Kiester and Childress in: Gorman, 1973).

Remarks: Several subspecies are recognised by Rummler and Fritz (1991), and the provenances of the karyotyped specimens were not specified.

***Cyclemys oldhamii* (Gray, 1863):**

Karyotype: $2n = 50-52$ (Kiester and Childress in: Gorman [1973]; as *Cyclemys dentata*: $2n = 52$

(Carr and Bickham, 1986: also as *Cyclemys dentata*; see Remarks).

Remarks: Fritz et al. (1997) attempted to revise the *Cyclemys dentata* complex, recognising four species in the complex. Of these, *C. oldhamii* Gray, 1863, occurs in the Indian region. The provenance of the karyotyped animals was not specified.

***Kachuga smithii* (Gray, 1863):**

Karyotype: $2n = 48-52$ (Sharma et al., 1975; Singh et al., 1972c: from northern India); $2n = 52$ (Killebrew, 1977).

***Kachuga tecta* (Bell in: Gray, 1831):**

Karyotype: $2n = 52$ (Singh, 1972c: from northern India).

***Melanochelys trijuga* (Schweigger, 1812):**

Karyotype: $2n = 50$ (DeSmet, 1978a); $2n = 52$ (Carr and Bickham, 1986; Sharma and Nakhasi, 1981: from India).

Remarks: Seven subspecies are recognized (see Das, 1995), but the provenance of the specimens karyotyped are unknown.

***Pyxidea mouhotii* (Gray, 1862):**

Karyotype: $2n = 52$ (Bickham and Carr, 1983).

TESTUDINIDAE

***Indotestudo elongata* (Blyth, 1853)**

Karyotype: $2n = 52$ (DeSmet, 1978a).

TRIONYCHIDAE

Aspideretes leithii (Gray, 1872) was reported to have 52 and 54 chromosomes by Singh et al. (1968a). However, this diploid number is actually derived from erroneously identified batagurids, and no karyological data are available for this trionychid species (Singh, 1972c).

***Lissemys punctata* (Bonnaterre, 1789)**

Karyotype: $2n = 66$ (Kiester and Childress in: Gorman, 1973; Singh et al., 1968a: from India; Stock, 1972).

SAURIA

EUBLEPHARIDAE

***Eublepharis macularius* (Blyth, 1854):**

Karyotype: $2n = 38$ (Gorman, 1973; DeSmet, 1981a; Szczerbak and Golubev, 1986 [the latter

captive-bred from animals originating from Pakistan; V. Manilo, pers. comm., 1998]).

GEKKONIDAE

Bunopus tuberculatus **Blanford, 1874:**

Karyotype: $2n = 42$ (Werner, 1956).

Remarks: Based on doubling of first meiotic metaphase.

Cosymbotus platyurus **(Schneider, 1792):**

Karyotype: $2n = 46$ (DeSmet, 1981a; Ota et al., 1987: from East Malaysia).

Remarks: Variation in centromeric positions of a few large pairs is evident between karyotypes reported by the above authors.

Crossobamon eversmanni **(Wiegmann, 1834):**

Karyotype: $2n = 42$ (Manilo, 1986).

Gekko gekko **(Linnaeus, 1758):**

Karyotype: $2n = 38$ (Cohen et al., 1967; Cohen and Clark, 1968; Singh, 1974b [from India]; DeSmet, 1981a; Wu and Zhao, 1984: from China; Solleder and Schmid, 1984; Schmid and Guttenbach, 1988).

Remarks: Cohen and Clark (1968), while confirming the standard diploid number of the species to be 38, reported the emergences of $2n = 39$ and 40 cytotypes in a cultured cell-line.

Gekko smithii **(Gray, 1842):**

Karyotype: $2n = 38$ (Ota, 1989a: from Sabah, East Malaysia).

Remarks: The $2n = 42$ karyotype of *Gekko smithii* reported from Thailand by Ota (1989a) was subsequently shown to belong to *G. taylori* [see Ota and Nabhitabhata, 1991], which appears to be a junior synonym of *G. siamensis* Ulber and Grossmann, 1990.

Hemidactylus brookii **Gray, 1845:**

Karyotype: $2n = 40$ (Bhatnagar, 1962: from India; Gorman, 1973; Olmo, 1981; DeSmet, 1981; Adegoke, 1985: from West Africa).

Hemidactylus bowringii **(Gray, 1845):**

Karyotype: $2n = 46$ (Nakamura, 1931; 1932: from Taiwan; Ota et al., 1989: from the Ryukyu Archipelago, Japan)

Hemidactylus flaviviridis **Rüppell, 1835:**

Karyotype: $2n = 40$ (Branch, 1980: from Oman; Singh, 1974b: from India); Singh and Bhatnagar, 1987a: from India; and $2n = 46$

(Asana and Mahabale, 1941: from India; Makino and Momma, 1949)

Hemidactylus frenatus **Duméril & Bibron, 1836:**

Karyotype: $2n = 46$ (Makino and Momma, 1949: but see below); $2n = 40$ (King, 1978: from northern Australia; Darevsky et al., 1984: from Vietnam; Kupriyanova et al., 1989: from Taiwan and the Ryukyu Archipelago, Japan; Ota et al., 1989: from Malaysia and Mariana); $2n = 3x = 60$ (Moritz and King, 1985: from Oceania).

Remarks: The $2n = 46$ karyotype reported by Makino and Momma (1949) is considered to be in error (see Kupriyanova et al., 1989).

Hemidactylus garnotii **Duméril & Bibron, 1836:**

Karyotype: $2n = 3x = 63$ (Moritz et al., 1993: from French Polynesia; Ota et al., 1995: from Hong Kong, eastern China); $2n = 3x = 42$ (Ota et al., 1996a: from Thailand), $2n = 3x = 70$ (Kluge and Eckardt, 1969: from Hawaii and Florida, USA).

Hemidactylus turcicus **(Linnaeus, 1758):**

Karyotype: $2n = 44$ (Werner, 1956: from Israel; Yaseen et al., 1995: from Egypt).

Lepidodactylus lugubris **(Duméril & Bibron, 1836):**

Karyotype: $2n = 3x = 63$ (Makino and Momma, 1949: from the Ogasawara Islands, Japan); $2n = 44$ (Cuellar and Kluge, 1972), $2n = 2x = 44$ and $2n = 3x = 66$ (Moritz and King, 1985; Volobouev and Pasteur, 1988; Volobouev et al., 1993: from French Polynesia).

Remarks: The reality of the difference between the triploid chromosome number of the Ogasawara population reported by Makino and Momma (1949) (as *Gehyra variegata ogasawarasimae*) and those reported for other populations by recent authors remains uncertain (Kluge, 1982; Ota, 1989).

Ptychozoon kuhli **Stejneger, 1902:**

Karyotype: $2n = 42$ (Ota and Hikida, 1988: from East Malaysia).

Teratoscincus scincus **(Schlegel, 1858):**

Karyotype: $2n = 36$ (Manilo, 1993: from Central Asia); $2n = 34$ (DeSmet, 1981a).

AGAMIDAE

***Bronchocela cristatella* (Kuhl, 1820):**

Karyotype: $2n = 48$ (Olmo, 1986); $2n = 34$ (Solleder and Schmid, 1988).

Remarks: Olmo (1986) listed the diploid chromosome number of this species, as well as of several other agamids, as a citation of Moody and Hutterer (1978), in which, however, no such data are given (see Ota and Hikida, 1989b). We suspect that the data were actually derived from Moody's (1980) unpublished thesis.

***Calotes emma* Gray, 1845:**

Karyotype: $2n = 34$ (Solleder and Schmid, 1988)

***Calotes jerdoni* Günther, 1871:**

Karyotype: $2n = 34$ (Sharma and Nakhasi, 1980: from north-eastern India).

***Calotes mystaceus* Duméril & Bibron, 1837:**

Karyotype: $2n = 34$ (Solleder and Schmid, 1988).

***Calotes versicolor* (Daudin, 1802):**

Karyotype: $2n = 32$ (DeSmet, 1981a); $2n = 34$ (Ganesh et al., 1997: from north-eastern India; Gorman, 1973; Singh, 1974b: from India; Olmo, 1981; Solleder and Schmid, 1988; Sharma and Nakhasi, 1980: from north-eastern India; Singh and Bhatnagar, 1987b: from northern India).

***Ceratophora stoddartii* Gray, 1834:**

Karyotype: $2n = 34$ (Olmo, 1986).

Remarks: See Remarks under *Bronchocela cristatella*.

***Cophotis ceylanica* Peters, 1861:**

Karyotype: $2n = 28$ (Olmo, 1986: from Sri Lanka).

Remarks: See Remarks under *Bronchocela cristatella*.

***Japalura variegata* Gray, 1853:**

Karyotype: $2n = 34$ (Dey et al., 1988: from northern India).

***Laudakia caucasica* (Eichwald, 1831):**

Karyotype: $2n = 34$ (Arronet, 1973: from Armenia; $2n = 36$ (Baig and Böhme, 1997: from Pakistan; Sokolovsky, 1875).

***Laudakia himalayana* (Steindachner, 1867):**

Karyotype: $2n = 36$ (Kupriyanova, 1984; Sokolovsky, 1975).

***Laudakia nupta* (De Filippi, 1843):**

Karyotype: $2n = 36$ (Baig and Böhme, 1997: from Pakistan; Olmo, 1986).

Remarks: See Remarks under *Bronchocela cristatella*.

***Laudakia tuberculata* (Hardwicke & Gray, 1827):**

Karyotype: $2n = 34$ (Baig and Böhme, 1997: from Pakistan; Dutt, 1969: from northern India)

***Lyriocephalus scutatus* (Linnaeus, 1758):**

Karyotype: $2n = 30$ (Moody and Hutterer, 1978: from Sri Lanka).

***Psammophilus dorsalis* (Gray in: Griffith & Pidgeon, 1831):**

Karyotype: $2n = 32$ (Rao and Aswathanarayana, 1979: from India).

***Ptyctolaemus gularis* (Peters, 1864):**

Karyotype: $2n = 34$ (Sharma and Nakhasi, 1980: from north-eastern India).

***Sitana ponticeriana* Cuvier, 1829:**

Karyotype: $2n = 36$ (Gorman, 1973); $2n = 44$ (Dutt, 1968: from northern India); $2n = 46$ (Witten, 1983; Makino and Asana, 1950b).

Remarks: Schleich and Kastle (1998a; 1998b) showed that this nominal species is actually a species complex. The provenance of some of the specimens karyologically investigated was not mentioned.

***Trapelus ruderatus* (Olivier, 1804)**

Karyotype: $2n = 46$ (Bhatnagar and Yoniss, 1976b: from Iraq).

***Uromastix hardwickii* Hardwicke & Gray, 1827:**

Karyotype: $2n = 34$ (Makino and Asana, 1950b); $2n = 36$ (Gorman, 1973; Singh, 1974b: from India; Sharma and Nakhasi, 1980b: from northern India).

SCINCIDAE

***Asymblepharus himalayanus* (Günther, 1864):**

Karyotype: $2n = 30$ (Duda and Gupta, 1981: from northern India).

Remarks: This taxon is usually referred to as *Scincella ladacensis himalayana* (see Ouboter, 1986). However, Das et al. (1998) allocated the species to the genus *Asymblepharus*.

***Chalcides ocellatus* (Forsskål, 1775):**

Karyotype: $2n = 26$ and $2n = 28$ (Caputo et al., 1993b: from Egypt; Dallai and Vegni Talluri, 1969: from Italy; $2n = 28$ (DeSmet, 1981b: from Egypt).

***Dasia olivacea* Gray, 1839:**

Karyotype: $2n = 32$ (Ota et al., 1996b: from East Malaysia).

***Eumeces schneideri schneideri* (Daudin, 1802):**

Karyotype: $2n = 32$ (Caputo et al., 1993a).

Remarks: Caputo et al. (1993a; 1994) and Kato et al. (1998) commented on the confusion of taxonomic treatment of *Eumeces schneideri* sensu lato in previous chromosomal studies.

***Lygosoma punctata* (Gmelin, 1799):**

Karyotype: $2n = 24$ (Bhatnagar, 1962: from northern India).

***Mabuya aurata* (Linnaeus, 1758):**

Karyotype: $2n = 32$ (Bhatnagar and Yoniss, 1976b: from Iraq; Ivanov et al., 1973: from India).

***Mabuya carinata* (Schneider, 1801):**

Karyotype: $2n = 30$ (Dutt, 1969: from India; Gorman, 1973); $2n = 32$ (Singh, 1974b: from India; Singh et al., 1968a: from India).

***Mabuya macularia* (Blyth, 1853):**

Karyotype: $2n = 26$ (Asana and Mahabale, 1941: from India; Olmo, 1981), $2n = 32$ (Makino and Asana, 1950a: from India; Olmo, 1981; Schmid and Guttenbach, 1988: from Thailand); $2n = 38$ (Ota et al., 1996b).

***Mabuya multifasciata* (Kuhl, 1820):**

Karyotype: $2n = 32$ (DeSmet, 1981b; Donnellan, 1991).

***Mabuya rudis* Boulenger, 1887:**

Karyotype: $2n = 32$ (Ota et al., 1996: from East Malaysia and Indonesia).

***Mabuya rugifera* (Stoliczka, 1870a):**

Karyotype: $2n = 32$ (Ota et al., 1996b: from Indonesia).

***Sphenomorphus indicus* (Gray, 1853):**

Karyotype: $2n = 28$ (Makino and Momma, 1949: from the central Ryukyu Archipelago, Japan, and Taiwan; Yang et al., 1989a: from Sichuan, China); $2n = 30$ (Ota and Lue, 1994: from Taiwan).

Remarks: Data provided by Makino and Momma (1949) appear problematic in terms of

species identity and accuracy in the counting of microchromosomes (see Ota and Lue, 1994).

LACERTIDAE

***Eremias gutturalis* (Lichtenstein, 1823):**

Karyotype: $2n = 38$ (Gorman, 1969; Kupriyanova, 1993: from Central Asia).

***Eremias persica* Blanford, 1875:**

Karyotype: $2n = 38$ (Ivanov et al., 1973: Olmo et al., 1990).

***Eremias velox* (Pallas, 1771):**

Karyotype: $2n = 38$ (Arronet, 1973: from Central Asia; Ivanov et al., 1973; Kupriyanova and Arronet, 1969; Olmo et al., 1990).

***Ophisops elegans* Ménétriés, 1832:**

Karyotype: $2n = 38$ (Arronet, 1968; 1973: from Central Asia; Gorman, 1969; Bhatnagar and Yoniss, 1976a; Olmo et al., 1990).

***Takydromus sexlineatus* Daudin, 1802:**

Karyotype: $2n = 38$ (Olmo et al., 1984; Odierna et al., 1985: from Thailand); $2n = 38, 40$ or 42 (Olmo et al., 1986: from Thailand); $2n = 40$, rarely 42 (Odierna et al., 1987: from Thailand); $2n = 42$ (Olmo et al., 1990).

VARANIDAE

***Varanus bengalensis* (Daudin, 1802):**

Karyotype: $2n = 40$ (Gorman, 1973; Singh, 1974b: from India; King and King, 1975; DeSmet, 1981b; Olmo, 1981).

***Varanus flavescens* (Hardwicke & Gray, 1827):**

Karyotype: $2n = 40$ (Gorman, 1973; Singh, 1974b: from India).

***Varanus griseus* (Daudin, 1803):**

Karyotype: $2n = 40$ (King and King, 1975; DeSmet, 1981b).

***Varanus salvator* (Laurenti, 1768):**

Karyotype: $2n = 40$ (King and King, 1975; DeSmet, 1981b).

SERPENTES

TYPHLOPIDAE

***Ramphotyphlops braminus* (Daudin, 1803):**

Karyotype: $2n = 3x = 42$ (Ota et al., 1991: from Taiwan and the central Ryukyu Archipelago, Japan; Wynn et al., 1987: from Seychelles, Hawaii and Florida, USA).

XENOPELTIDAE

Xenopeltis unicolor Boie, 1827:

Karyotype: $2n = 36$ (Cole and Dowling, 1970).

ACROCHORDIDAE

Acrochordus granulatus (Schneider, 1799):

Karyotype: $2n = 36$ (Sharma et al., 1980a: from western India).

BOIDAE

Eryx conicus (Schneider, 1801):

Karyotype: $2n = 34$ (Singh, 1972a: from India; DeSmet, 1978b).

Eryx johnii (Russell, 1801):

Karyotype: $2n = 34$ (Singh et al., 1968: from northern India).

Python molurus (Linnaeus, 1758):

Karyotype: $2n = 36$ (Singh et al., 1968a; 1968c: from India).

COLUBRIDAE

Ahaetulla nasuta (Lacepède, 1789):

Karyotype: $2n = 36$ (Singh, 1974a: from India; Sharma and Nakhasi, 1980: from India; Sharma et al., 1980a: from eastern India).

Amphiesma stolatum (Linnaeus, 1758):

Karyotype: $2n = 36$ (Rossman and Eberle, 1977; Singh, 1972a: from India).

Argyrogena fasciolata (Shaw, 1802):

Karyotype: $2n = 36$ (Ray-Chaudhuri et al., 1971; Singh, 1972a: from India).

Boiga forsteni (Duméril, Bibron & Duméril, 1854):

Karyotype: $2n = 36$ (Ray-Chaudhuri et al., 1971: from India; Singh, 1972a; from India).

Boiga trigonata (Schneider in: Bechstein, 1802):

Karyotype: $2n = 36$ (Ray-Chaudhuri et al., 1971: from India; Singh, 1972a: from India).

Cerberus rynchops (Schneider, 1799):

Karyotype: $2n = 36$ (Gorman, 1973; Ray-Chaudhuri et al., 1971: from India; Singh, 1972a: from India); $2n = 38$ (Gorman, 1973).

Chrysopelea ornata (Shaw, 1802):

Karyotype: $2n = 36$ (Singh, 1974a: from India); $2n = 40$ (Sharma et al., 1980: from eastern India).

Dendrelaphis pictus (Gmelin, 1789):

Karyotype: $2n = 36$ (Sharma et al., 1980a: from eastern India).

Remarks: As *Dendrelaphis ahaetulla*.

Elaphe mandarina (Cantor, 1842):

Karyotype: $2n = 38$ (Wei et al., 1992: from China; Yang et al., 1989a: from China).

Elaphe radiata (Schlegel, 1837):

Karyotype: $2n = 30$ (Schmid and Guttenbach, 1988).

Elaphe taeniura (Cope, 1861):

Karyotype: $2n = 36$ (Xie et al., 1983: from China).

Enhydryis enhydryis (Schneider, 1799):

Karyotype: $2n = 36$ (Sharma and Nakhasi, 1980a: from north-eastern India; Sharma et al., 1980: from north-eastern India).

Gerarda prevostiana (Eydoux & Gervais, 1837):

Karyotype: $2n = 36$ (Ray-Chaudhuri et al., 1971: from India; Singh, 1972a: from India).

Lycodon aulicus (Linnaeus, 1758):

Karyotype: $2n = 36$ (Nakamura, 1935; Ray-Chaudhuri et al., 1971: from India; Singh, 1972a: from India).

Natrix tessellata (Laurenti, 1768):

Karyotype: $2n = 34$ (Kobel, 1967).

Oligodon arnensis (Shaw, 1802):

Karyotype: $2n = 46$ (Bhatnagar, 1959: from India).

Pseudoxenodon macrops (Blyth, 1854):

Karyotype: $2n = 38$ (Yang et al., 1989b: from China).

Ptyas korros (Schlegel, 1837):

Karyotype: $2n = 36$ (Xiong et al., 1982: from China).

Ptyas mucosus (Linnaeus, 1758):

Karyotype: $2n = 36$ (Ray-Chaudhuri et al., 1970: from India); $2n = 34$ (DeSmet, 1978b; Singh, 1972a: from India).

Xenochrophis piscator (Schneider, 1799):

Karyotype: $2n = 40$ (Sharma and Nakhasi, 1980a: from north-eastern India; Singh et al., 1968b: from north-eastern India); $2n = 42$ (DeSmet, 1978b; Singh et al., 1968a: from northern India).

Zaocys nigromarginatus (Blyth, 1854):

Karyotype: $2n = 34$ (Yang et al., 1989b: from China).

Remarks: Nakamura (1935) referred material from Taiwan with $2n = 36$ chromosomes to *Zaocys nigrorginatus* (sic for *nigromarginatus*) *oshimai* Stejneger, 1925, although the subspecies is actually synonymous with *Z. dhumnades* (Cantor, 1842); see Ota (1991).

ELAPIDAE

Bungarus caeruleus (Schneider, 1801):

Karyotype: $2n = 44$ (males); $2n = 43$ (females) (Ray-Chaudhuri et al., 1970: from India; Singh et al., 1970; 1979: from India).

Remarks: Ray-Chaudhuri et al. (1970) and Singh et al. (1970; 1979) revealed numerical heterogamety in the female karyotype of this species, which is involved by multiple sex-chromosome constitution.

Bungarus fasciatus (Schneider, 1801):

Karyotype: $2n = 38$ (Singh, 1974a: from India; Toriba, 1987: from China and Thailand).

Remarks: Toriba (1987) demonstrated variation in centromeric position of W-chromosome between Indian and Chinese-Thai populations.

Naja kaouthia Lesson, 1831:

Karyotype: $2n = 38$ (Ray-Chaudhuri et al., 1971: from India; Singh, 1972a: from India).

Naja naja (Linnaeus, 1758):

Karyotype: $2n = 38$ (Ray-Chaudhuri et al., 1970: from India; Singh, 1972a; from India).

Remarks: Dutt (1966) reported extensive variation of the diploid number (i.e., $2n = 36-41$: involving aneuploidy) in germ cells of a male from northern India.

HYDROPHIIDAE

Enhydrina schistosa (Daudin, 1803):

Karyotype: $2n = 32$ (male); $2n = 33$ (female) (Ray-Chaudhuri et al., 1971: from India; Singh, 1972b: from India).

Remarks: Both the above workers reported multiple sex-chromosome complex for the female karyotype.

Hydrophis cantoris Günther, 1864:

Karyotype: $2n = 35$ (female) (Singh, 1972a: from India).

Hydrophis cyanocinctus Daudin, 1803:

Karyotype: $2n = 32$ (male) and $2n = 33$ (female) (Singh, 1972a: from India); $2n = 36$ (both sexes) (Zheng and Hong, 1983: from eastern China).

Remarks: Singh (1972a) considered numerical heterogamety in female karyotype as indicative of the presence of multiple W-chromosomes (i.e., W1 and W2).

Hydrophis fasciatus (Schneider, 1799):

Karyotype: $2n = 35$ (female) (Singh, 1972a: from India).

Remarks: Singh (1972a) considered numerical heterogamety in female karyotype as indicative of the presence of multiple W-chromosomes (i.e., W1 and W2).

Hydrophis gracilis (Shaw, 1802):

Karyotype: $2n = 35$ (Singh, 1972a: from India).

Remarks: Singh (1972a) considered numerical heterogamety in female karyotype as indicative of the presence of multiple W-chromosomes (i.e., W1 and W2).

Hydrophis ornatus (Gray, 1842):

Karyotype: $2n = 32$ (Singh, 1972a; 1974a: from India).

Hydrophis spiralis (Shaw, 1802):

Karyotype: $2n = 32$ (female) (Ray-Chaudhuri et al., 1971: from India; Singh, 1972a: from India).

Kerilia jerdonii Gray, 1849:

Karyotype: $2n = 32$ (Singh, 1974a: from India).

Laticauda laticaudata (Linnaeus, 1758):

Karyotype: $2n = 40$ (Gorman, 1981: from the Philippines; Toriba and Yoshida, 1986: from the Ryukyu Archipelago, Japan).

Laticauda colubrina (Schneider, 1799):

Karyotype: $2n = 34$ (Gorman, 1981: from the Philippines; Toriba and Yoshida, 1986: from the Ryukyu Archipelago, Japan).

Pelamis platurus (Linnaeus, 1766):

Karyotype: $2n = 38$ (Gutiérrez and Bolaños, 1980: from Costa Rica; Zheng and Hong, 1984: from eastern China).

Praescutata viperina Schmidt, 1852:

Karyotype: $2n = 32$ (Ray-Chaudhuri et al., 1971: from India; Olmo, 1981).

VIPERIDAE

***Daboia russelii* (Shaw & Nodder, 1797):**

Karyotype: $2n = 36$ (Cole, 1990; Singh, 1974a: from India; Zhang and Hong, 1984: from eastern China).

***Echis carinatus* (Schneider, 1801):**

Karyotype: $2n = 36$ (Cole, 1990; DeSmet, 1978a; Singh, 1972a: from India; Singh et al., 1968a: from India).

Remarks: DeSmet (1978b) described the diploid number 34 in the text, but provided figures that indicated a value of 36.

***Macrovipera lebetina* (Linnaeus, 1758):**

Karyotype: $2n = 36$ (Cole, 1990; DeSmet, 1978b).

***Trimeresurus erythrurus* (Cantor, 1839):**

Karyotype: $2n = 36$ (Toriba, 1994: from Myanmar).

***Trimeresurus mucrosquamatus* (Cantor, 1839):**

Karyotype: $2n = 36$ (Cole, 1990; Nakamura, 1935: from Taiwan; Qu et al., 1981: from continental China).

***Trimeresurus stejnegeri* Schmidt, 1927:**

Karyotype: $2n = 36$ (Nakamura, 1935; Qu et al., 1981: from China).

Remarks: Nakamura (1935) referred his material from Taiwan to *Trimeresurus gramineus stejnegeri*. However, subsequent taxonomic studies revealed that both *gramineus* and *stejnegeri* are valid species, and the former does not occur in Taiwan (see Ota [1991], for a review). The systematics of the green species of *Trimeresurus* is unclear (Malhotra and Thorpe, "1997" 1996), and at present, many species are assigned to *T. gramineus*.

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COMMENTS ON DISTRIBUTIONAL RECORDS OF REPTILES FROM GUJARAT STATE

A few recent environmental impact assessment (EIA) and biodiversity reports pertaining to Gujarat State have yielded putatively new distributional records of reptiles.

According to Singh and Kamboj (1966), the gecko *Cyrtopodion kachhensis* is common in the Gir forest, Junahadh District. This is an arid habitat species, known only from the Kutch District of Gujarat, western India (Smith, 1935). The present record does not match the known habitat of the species, and I have never seen it in the Gir forest. The new record may be based on misidentified *Hemidactylus brookii*, whose external morphological characteristics is similar to that of *C. kachhensis*.

Hemidactylus maculatus occurs in the Surat-Dangs District of Gujarat, southwards to Maharashtra, Kerala and Tamil Nadu. The report of the species from Mundra and Mandvi Tehsils of Kutch District by Anon (1997) may be the result of inaccurate identification. On the basis of description of the species in Smith (1935), females of *H. maculatus* and *H. brookii* differ only in the arrangement of lamellae on the toes.

Calotes rouxii is known to be restricted to the Western Ghats (Smith, 1935; Das, 1994). The species has been recorded subsequently from the Shoolpaneswar Wildlife Sanctuary, Bharuch (Naik et al., 1993; Vyas, 1995) and most recently, I collected specimens from the forests of Kevadi (Chhota Udepur), in Vadodara District and Ratanmahal, in Panchmahal District. The record in Anon (1997) from near Desalpur, Bhuj-Kutch District, appears doubtful, in view of the arid habitat conditions of the new locality.

Members of the family Uropeltidae are restricted to high rainfall areas of the Western Ghats and adjacent portions of the Eastern Ghats of peninsular India, besides Sri Lanka. *Uropeltis occellatus* is known to occur in the forests of the Nilgiris and Anaimalais, at altitudes between 600-1,000 m (Smith, 1935; Rajendran, 1985).

The report from Shoolpaneswar Wildlife Sanctuary, Bharuch District, by Sabnis and Amin (1992) and Naik et al. (1993) is not only at a considerable distance from the known range of the species, it is also within the dry zone.

Patel and Reddy (1995) reported *Oligodon venustus* from between the Narmada and Sabarmati Rivers, without mentioning any specific locality. This species is found only in the Western Ghats, south of the Goa Gap (Smith, 1943), and the Gujarat record is therefore probably in error.

The new distributional records of *Cyrtopodion kachhensis*, *Hemidactylus maculatus*, *Calotes rouxii*, *Uropeltis ocellatus* and *Oligodon venustus* from Gujarat State are therefore based on unsubstantiated reports, and there appears to be no voucher specimens. If these reports are true, it would suggest that such habitats and populations are important.

The reports cited raise the question of trustworthiness of unrefereed publications and such types of EIA reports might be problematic for conservation and management. As per Das et al. (1996), "Distribution is also an important component of the biology of the species: if we fail to note its precise distributional range, we may fail to understand its ecological requirements".

While on the subject, it is worth reiterating the plea of Brown (1992): "Accurate information on existence and distributions of species requires an expert knowledge of the animals, geography and the literature".

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RAJU VYAS, Sayaji Baug Zoo, Vadodara, Gujarat 390 018, India.

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Morphometry of major visceral organs of male *Daboia russelii*

Visceral anatomy of snakes have been studied by several workers (e.g., Bergman, 1961; Davis, 1981; Swaminathan et al., 1995; see Parsons and Cameron, 1977, for a review). There is little published information on the anatomy of the Russell's viper, *Daboia russelii*, a common venomous snake in India. A study was conducted to briefly outline the anatomical disposition of the major visceral organs in male *D. russelii*.

Four *Daboia russelii* which had died without specific etiology at the Arigna Anna Zoological Park, Chennai, southern India, were preserved in 10% formalin after taking body measurements. The ventral scales were counted. A ventral median incision was made to expose the visceral organs. The number of ribs were counted. The morphology and position of major visceral organs were described in relation to the ribs.

The total lengths of the snakes were 126.5 cm, 126.0 cm, 126 cm and 127.0 cm. Ventral scale counts were 173 in all four specimens. The size and relative position of the visceral organs are summarized in Table 1.

Digestive system.- The alimentary canal extends from the pharynx to cloaca. The oesophagus passes on the left of the visceral cavity. The anterior part of the oesophagus was thin walled, gradually becoming thicker towards the stomach and continued as a dilated, thick-walled stomach placed on the left side of the stomach cavity. The stomach was highly muscular, with cardia, fundic and pyloric regions. The pyloric end is funnel shaped with abrupt constriction from where it continue as duodenum. Cystic and pancreatic ducts open into the duodenum. The small intestine is arranged in a large number of coils and extends in the direction of the axis of the body. At the transition to the large intestine, the rectal caecum is absent, but a sigmoid flexure is present and the rest continue, terminating into a cloaca. The liver is bilobed- left, and right (plus tail on right lobe). Left and right lobes form a cleft anteriorly in which the apex of the heart is lodged. From the posterior end of the right lobe, the liver tail extends as an elongated lobe posteriorly.

Cystic duct extends from the posterior extremity of the liver and terminates in a gall bladder. Pancreas is pear-shaped and located on the right side of the duodenum and on the ventral aspect of the gall bladder. Spleen is a small nodule at the cleft of the pancreas.

Respiratory system.- The trachea extends as a cartilaginous tube from the larynx and the right lung is developed and located dorsal to either side of the trachea. The anterior part of the lungs are vascular while the posterior part is saccular adjacent to the heart and anterior part of the liver.

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Four *Daboia russelii* which had died without specific etiology at the Arigna Anna Zoological Park, Chennai, southern India, were preserved in 10% formalin after taking body measurements. The ventral scales were counted. A ventral median incision was made to expose the visceral organs. The number of ribs were counted. The morphology and position of major visceral organs were described in relation to the ribs.

The total lengths of the snakes were 126.5 cm, 126.0 cm, 126 cm and 127.0 cm. Ventral scale counts were 173 in all four specimens. The size and relative position of the visceral organs are summarized in Table 1.

Digestive system.— The alimentary canal extends from the pharynx to cloaca. The oesophagus passes on the left of the visceral cavity. The anterior part of the oesophagus was thin walled, gradually becoming thicker towards the stomach and continued as a dilated, thick-walled stomach placed on the left side of the stomach cavity. The stomach was highly muscular, with cardia, fundic and pyloric regions. The pyloric end is funnel shaped with abrupt constriction from where it continue as duodenum. Cystic and pancreatic ducts open into the duodenum. The small intestine is arranged in a large number of coils and extends in the direction of the axis of the body. At the transition to the large intestine, the rectal caecum is absent, but a sigmoid flexure is present and the rest continue, terminating into a cloaca. The liver is bilobed- left, and right (plus tail on right lobe). Left and right lobes form a cleft anteriorly in which the apex of the heart is lodged. From the posterior end of the right lobe, the liver tail extends as an elongated lobe posteriorly.

Cystic duct extends from the posterior extremity of the liver and terminates in a gall bladder. Pancreas is pear-shaped and located on the right side of the duodenum and on the ventral aspect of the gall bladder. Spleen is a small nodule at the cleft of the pancreas.

Respiratory system.— The trachea extends as a cartilaginous tube from the larynx and the right lung is developed and located dorsal to either side of the trachea. The anterior part of the lungs are vascular while the posterior part is saccular adjacent to the heart and anterior part of the liver.

TABLE 1: Data on topography (in mm and % body length) of male *Daboia russelii*.

Sl.	Organ	1	2	3	4	Mean	% body	Position (in relation to ribs)
1	Body length	1270	1260	1265	1260	1263.75	100	-
2	Oesophagus	467	463	466	464	465	367	1-91
3	Trachea	370	330	360	340	350	276	1-68
4	Heart	35 x 20	25 x 20	30 x 22	30 x 18	30 x 20	23	59-68
5	Liver (left)	136 x 10	134 x 10	135 x 10	135 x 10	135 x 10	106	67-85
6	Liver (right)	114 x 10	113 x 7	113 x 8	112 x 7	113 x 8	89	70-83
7	Liver (tail)	55 x 10	55 x 10	55 x 10	55 x 10	55 x 10	43	85-92
8	Intestine	330	330	330	330	330	261	105-171
9	Spleen	2 x 2	2 x 2	2 x 2	2 x 2	2 x 2	1	105-106
10	Stomach (greatest curvature)	102	98	100	100	100	79	91-105
11	Stomach (least curvature)	67	65	65	63	65	51	
12	Stomach (width at fundus)	25	22	23	22	23	18	
13	Gall bladder	30 x 19	30 x 17	30 x 18	30 x 18	30 x 18	23	103-108
14	Pancreas	19 x 40	15 x 40	18 x 40	16 x 40	17 x 40	13	103-107
15	Testes (left)	11	9	10	10	10	7	122-128
16	Testes (right)	11	10	9	10	10	7	112-118
17	Kidney (left)	190	170	184	176	180	142	136-162
18	Kidney (right)	141	125	136	131	133	105	130-156

Urinogenital system.- The kidneys are paired, multilobed and asymmetrical. The number of lobes in the right kidney is 23, whereas in the left is 21 for all four specimens. The urinary and seminal ducts continue as a common channel across papilla urogenitalis into the cloaca. Testes present asymmetrically in the posterior aspect of the abdominal cavity.

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S. SWAMINATHAN¹, R. THIRUTHALINATHAN¹, J. VENKATESH² and P. S. LALITHA²

¹Arignar Anna Zoological Park, Vandalur, Chennai, India; ²Madras Veterinary College, Chennai 600 007, India.

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A PHOTOGRAPHIC GUIDE TO SNAKES AND OTHER REPTILES OF PENINSULAR MALAYSIA, SINGAPORE AND THAILAND by Merel J. Cox, Peter Paul van Dijk, Jarujin Nabhitabhata and Kumthorn Thirakhupt. 1998. ISBN 1 85368 438 4. New Holland Publishers (UK) Ltd., 24 Nutford Place, London, W1H 6DQ, U.K. Fax: 0171-724-6184. Price £ 9.99. Distributed in Thailand by Asia Books Co. Ltd., 5 Sukhumvit Road, Soi 61, P.O. Box 40, Bangkok 10110, Thailand. Price 395 Thai Baht.

The wonderful herpetofauna of mainland south-east Asia, subject of several scientific monographs and books, was not accessible to the common man. Who better to write a readable and well illustrated text than Jack Cox, Peter Paul van Dijk, Jarujin Nabhitabhata and Kumthorn Thirakhupt: names everybody who works on, or has in interest in, south-east Asian herpetology, are familiar with? Their long-awaited field guide to the 222 species of reptiles (crocodiles, turtles, lizards and snakes) found in the erstwhile Kingdom of Siam (now Thailand) and Malaya (at present West Malaysia and Singapore) is finally out.

The work includes an introduction, tips on how the work is to be used, description of reptile habitats in the area covered by the book, hints on finding, identifying and recording reptiles, conservation and protection of reptiles, snake-bite and its treatment, the species descriptions, glossary, further reading and an index of both English and scientific names.

In all, about half of the known fauna has been dealt with. For each of the selected species, there is at least one (and sometimes two or more) colour photo, showing the animal in life. For species that vary in colouration, either as adults (such as *Naja kaouthia*) or as juveniles, there are additional photographs. The text is short, and includes a suggested English name, the valid scientific name, maximum length recorded, followed by a short description that will be useful for quick field identification, as well as brief natural history notes, including clutch size, habitat and conservation status. The photographs have

been gathered from a large number of colleagues. The quality of the photos ranges from good to superb, and in here is my only complaint—I wish the size of the book was bigger, to enjoy the wonderful snake and other reptile photographs more!

An additional small point is the absence of the citation of the work of Boulenger (1912) in the bibliography provided at the end of the work—this is arguably the most important work on the subject for Peninsular Malaya. However, the publishers thought that pre-1970 literature would be unavailable to the general readership of the book (P. P. van Dijk, pers. comm., 1998).

This pocket guide is arguably New Holland's best in their growing series on the world's "snakes and other reptiles", and will surely become a backpacker's item, as travel industry in south-east Asia continues to burgeon. And given the large number (290) of colour photos, at a mere £ 9.99, to use an old cliché, this book is good value for money.

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BOULENGER, G. A. 1912. A vertebrate fauna of the Malay Peninsula from the Isthmus of Kra to Singapore including the adjacent islands. Reptilia and Batrachia. Taylor and Francis, London. xiii + 294 pp.

Indraneil Das
Institute of Biodiversity and Environmental Conservation, Universiti Malaysia Sarawak, 94300 Kota Samarahan, Sarawak, East Malaysia. Email: idas@mailhost.unimas.my

REPTILES OF MONGOLIA. AMPHIBIANS AND REPTILES OF MONGOLIA. THE VERTEBRATES OF MONGOLIA by Natalia Ananjeva, Kh. Munkhbayar, Nikolai Orlov, V. F. Orlova, D. V. Semenov and Kh. Terbish. 1997. KMK Ltd., Moscow. 416 pp. Available from Dr. Natalia Ananjeva, Division of Terrestrial Vertebrates, Zoological Institute, Russian Academy of Sciences, St. Petersburg 199034, Russia. Fax: + 812 114 0444; Email: nbanorus@glas.apc.org. ISBN 5-87317-040-1. Price: US\$ 20.

Mongolia's biodiversity was subjected to intensive investigation by a team of Mongolian and Russian biologists in between 1970 and 1990s at the South Gobi Field Station Ekhiyn-Gol. The result was a series of publications entitled 'The Vertebrates of Mongolia', of which the volume under review is a component.

The text is entirely in Russian, except for a three page English summary at the end. The contents include: an introduction, materials and methods, leading straight on to the species accounts, each written by one or more of the four authors of the volume. Species accounts include descriptions (including squamation and size), synonymy, karyotypes, distributional ranges, details of ecology (sometimes illustrated with ethograms, pie charts and bar diagrams) and black-and-white photographs of live and preserved animals to show shape and colour variation, as well as photographs of habitats. Captions to figures are both in Russian and English. The heart of the work also contains a general account

of the reptiles of the country, including biogeography and short review of ecological relationships of species. In all, 21 species are shown as occurring in Mongolia, including three gekkonids, three agamids, seven lacertids, a boid, five colubrids and at least two viperids (the occurrence of a third, *Vipera ursini* is doubtful, with no specific records from the country).

The References cited section includes works in Russian as well as English, two appendices (on physiographic features of Mongolia and details of lizards collected from various stations under the project) and finally, an English summary.

One hopes this significant work will be translated into English and widely distributed.

Indraneil Das

Institute of Biodiversity and Environmental Conservation, Universiti Malaysia Sarawak, 94300 Kota Samarahan, Sarawak, East Malaysia. Email: idas@mailhost.unimas.my

BIOGEOGRAPHY OF THE REPTILES OF SOUTH ASIA by Indraneil Das. 1996. Krieger Publishing Company, Malabar, Florida. Hardcover. 87 pp. Available from Krieger Publishing Company, P. O. Box 9542, Melbourne, Florida 32902-9542, USA. Price US\$ 27.50.

Considering the wide scope of the title, this is actually a slim volume containing only about 35 pages of text and 40 pages of tables. However, a lot of good, current material is packed into this little book on a subject which is surprisingly neglected in our region.

The last major work on reptile biogeography of south Asia was that of K. C. Jayaram (1974), who reported (sometimes mistakenly) on the ecology and distribution of some Indian reptiles. Prior to this, S. L. Hora's (1949) Satpura hypothesis argued that the spread of Malayan taxa to the

Western Ghats in India was via a once heavily forested corridor of the Siwalik hills. Since the theory lacks geological evidence, Das reports the general conclusion that the distribution of many Indian taxa of plants and animals with an affinity to south-east Asia reflects the remains of an ancient, wider distribution.

The author includes a useful, updated checklist of 631 species of reptiles in 185 genera and of these 63.7% are endemic to the region. He identifies 10 physiogeographic zones and points to the highest species diversity in the high rainfall

zones, including Sri Lanka, Western Ghats, Northeast and the Himalayas. Distribution data reveals that few indigenous Indian taxa are found extraliminally, being largely of the non-emigrant type. Predictably, emigrant reptiles from the Indo-Malayan region, are reported to use niches unoccupied by the local species; specific examples of these taxa and their niches would have been valuable.

Tables include "Composition and Endemicity of the Reptiles of South Asia", "Affinities of the Non-endemic Reptile Genera", and "Species Pairs of Reptiles". The latter includes the presumed mode of speciation. Of the small sample examined (26 species), the dispersal speciation mode accounts for 53.9%, vicariance mode 38.5% and the refugial mode for 7.7%.

Other interesting conclusions arise in this work, including the affinities between the physiographic zones. For example, the Andaman and Nicobar groups (Bay Islands) are sister areas, as are the Western Ghats with Sri Lanka and the Eastern Ghats with the Deccan. The reptile fauna of the dry northwest is dissimilar to the rest of the region. The fauna of the northeast is found not to be similar to that of the Western Ghats, which is at variance with Hora's Satpura Hypothesis.

It is abundantly evident that this book and the work from which much of the material is derived, will be the basis on which an accurate biogeographical theory for the region can be evolved. Despite the paucity of herpetological

work here, new species are continually being described from the region. This book provides a strong motivation for further ecological and biogeographical work is expected to unravel questions of reptile speciation, dispersal and colonization in south Asia.

The book is frontispiced with 16 pages of excellent colour plates: a mixed bag of the very common (*Naja naja*) to the rare (*Batagur baska*).

The book ends with references and a brief index. Aside from some minor typo and usage errors, this is a well produced volume and the binding will likely withstand the rigors of the south Asian climate. "The Biogeography of the Reptiles of South Asia" should attract a wide readership, from herpetologists to students of evolution and ecology.

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Romulus Whitaker

Centre for Herpetology, Madras Crocodile Bank Trust, Post Bag 4, Mamallapuram, Tamil Nadu 603 104, India.

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